Volume 58, Number 1

February 1984

Northwest Science

CONTENTS

1 A Late Quaternary Chronology of Mass Wasting for a Small Valley in the Lemhi Mountains of Idaho
David R. Butler

14 Lead Concentrations in Ruffed Grouse Collected from Southwestern Virginia
Ronald J. Kendall, Gary W. Norman, and Patrick F. Scanlon

18 Analysis of Surface Pollen from Alberta, Canada, by Polar Ordination
Richard G. Holloway

29 An Approach to Classifying Seral Vegetation within Habitat Types
Robert Steele

40 Distribution, Abundance, and Nesting Characteristics of Snowy Plovers on the Oregon Coast
Ruth Wilson-Jacobs and E. Charles Meslow

49 Histology of **Cowania stansburiana** Actinorhizae
David L. Nelson and Pattie L. Schuttler

57 Early Plant Succession on Pinyon-Juniper Controlled Burns
Richard L. Everett and Kenneth Ward

69 The Recent History and Present Distribution of the Red Fox in Washington
Keith B. Aubry

80 Vegetation Types Used by Mule Deer Fawns, Mid-Columbia River, Washington
Paul C. Fielder and Charles E. McKay, Jr.

79 Meetings

79 1983 Manuscript Reviewers

Quarterly Publication of the Northwest Scientific Association

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science*, is open to individuals for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 300 students or more $40. All other subscribers, $15 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

John W. Weber
Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164-2910

Officers of the Association

President Stephen F. Arno
USDA Forest Service
Missoula, Montana (1984)*

Vice-President Oscar Sziklai
University of British Columbia
Vancouver, B.C. (1984)

Secretary Robert L. Carr
Eastern Washington University
Cheney, Washington (1984)

Treasurer Steven J. Brunsfeld
College of Forestry, Wildlife, and Range Sciences
University of Idaho
Moscow, Idaho 83843 (1986)

Past President John Perkins
The Evergreen State College
Olympia, Washington (1984)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Black
University of British Columbia
Vancouver, British Columbia
(1985)

Donald Hanley
University of Idaho
Moscow, Idaho (1986)

Warren Iliff
Washington Park Zoo
Portland, Oregon (1986)

Susan Kephart
Willamette University
Salem, Oregon (1986)

Denis P. Lavender
Oregon State University
Corvallis, Oregon (1984)

Don Minore
U.S. Forest Service
Corvallis, Oregon (1984)

Richard J. Naskali
University of Idaho
Moscow, Idaho (1984)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

Steven R. Seavey
Lewis and Clark College
Portland, Oregon (1985)

Robert Stockhouse
Pacific University
Forest Grove, Oregon (1986)

Kareen Sturgeon
Linfield College
McMinnville, Oregon (1985)

B. J. Verts
Oregon State University
Corvallis, Oregon (1986)

Robert Zasoski
University of Washington
Seattle, Washington (1984)

*Term of office expires in the year given in parentheses.

PRINTED QUARTERLY (FEBRUARY, MAY, AUGUST, AND NOVEMBER) BY THE WASHINGTON STATE UNIVERSITY PRESS, OFFICE OF PUBLICATIONS, PULLMAN, WASHINGTON 99164-5910.

David R. Butler

Department of Geography
Oklahoma State University
Stillwater, Oklahoma 74078

A Late Quaternary Chronology of Mass Wasting for a Small Valley in the Lemhi Mountains of Idaho

Abstract

Mapping of landforms and collection of relative-age data identified the type and age of late Quaternary deposits attributable to periods of cold climate in a small valley in the Lemhi Mountains. Mass wasting, rather than glaciation, characterized the Holocene geomorphic responses to decreasingly severe cold episodes. Pleistocene responses probably included both glaciation and development of periglacial slope movement over permafrost. Climatic changes were relatively synchronous throughout the Lemhi Mountains, but geomorphic responses differed within individual valleys.

Introduction

The last two decades have seen a remarkable expansion in our understanding of the chronology of glacial and mass-wasting periods in the Rocky Mountains. From the time of Richmond's (1965) classic paper outlining five Pleistocene and two Holocene glacial episodes in the Rockies to the present, research has expanded and refined the number and timing of glacial and cold climatic episodes. Table 1 presents a composite chronology for the Colorado and Wyoming Rocky Mountains, as drawn from a variety of works (Richmond 1965, Pierce *et al.* 1976, Madole 1980, Benedict 1981).

Research in the mountains of Idaho has also expanded our knowledge of the late Quaternary chronology. The Lemhi Mountains of east-central Idaho, approximately 160 km west of Yellowstone National Park, have been a focus of such work in recent years (Fig. 1). Building on the preliminary chronologies of Ruppel and Hait (1961) and Dort (1962), Knoll (1977) produced a detailed composite late Quaternary glacial and mass wasting chronology from four valleys in the Lemhi Mountains. His chronology contains one pre-Bull Lake, three Bull Lake, and nine Pinedale glacial advances. Knoll also documented five separate cold climatic pulses that occurred during the Neoglacial (the last 5000 years) on the basis of both glacial and mass wasting deposits. He correlated these five pulses with the three generally accepted Neoglacial stages of Wyoming and Colorado (Table 1). Recently, Winter (1982) further documented the latest Neoglacial stade through tree-ring analysis, indicating a major treeline retreat in the southern Lemhi Mountains 300 to 500 years BP (before present).

Geographic Setting and Background for the Present Study

The specific study site for the present paper is a short, 1.2 km long, unnamed valley on the eastern side of the central portion of the Lemhi Mountains. The valley is unofficially called the Hilltop Valley, after a mining claim near the valley head (Figs. 1 and 2).

The Hilltop Valley is much shorter than other major valleys in the Lemhi Mountains (Dort 1962, Knoll 1977). It is also relatively narrow, ranging in width from

260 to 300 m. The valley head is a poorly developed and/or preserved natural amphitheater at an elevation of approximately 2700 m above sea level. The base of a large terminal ridge that encloses the end of the valley is at an elevation of about 2350 m, providing a valley gradient of 291 m/km. This gradient is much steeper than in nearby valleys (Knoll 1977, Butler 1982).

The topoclimatic conditions of the Hilltop Valley are not as favorable for glaciation as those found in nearby valleys (Knoll 1977, Butler 1982). The Hilltop Valley is oriented almost exactly North 45° East, about 20° more easterly than an adjacent glaciated

TABLE 1. Comparison of the Composite Glacial Chronology for Colorado and Wyoming with Knoll's Chronology for the Lemhi Mountains of Idaho.

		Composite Chronology for the Colorado and Wyoming Rocky Mountains	Knoll's Composite Chronology for the Lemhi Mountains
HOLOCENE	Neoglaciation (5,000 BP-Present)	Arapaho (or Gannett) Peak Advance (350-100 BP) Audubon Advance (2,400-900 BP) Triple Lakes Advance (5,000-3,000 BP)	Stade 5 Stade 4 Stade 3 Stade 2 Stade 1
	10,000 BP-5,000 BP	Ptarmigan Advance (7,250-6,600 BP) Satanta Peak Advance (Approx. 10,000 BP)	No advances recorded
PLEISTOCENE	Pinedale Glaciation (35,000-10,000 BP)	4 (No precise dating 3 for these four 2 advances) 1	9 8 7 (No precise dating 6 for these nine 5 advances) 4 3 2 1
	Bull Lake Glaciation (Approx. 140,000 BP)	At least two advances	3 (No precise dating 2 for these three 1 advances)
	Pre-Bull Lake Glaciations (No firm dates)	Sacagawea Ridge Cedar Ridge Washakie Point	1 (No precise dating or correlation available)

valley. The headwall is poorly shaded as well, and its base is almost 200 m lower in elevation than the modestly glaciated valley immediately to the south (Butler 1982).

The Hilltop Valley headwall is composed of Ordovician Kinnikinic quartzite (Hait 1965). This bedrock is somewhat jointed and fractured, with snow accumulating in

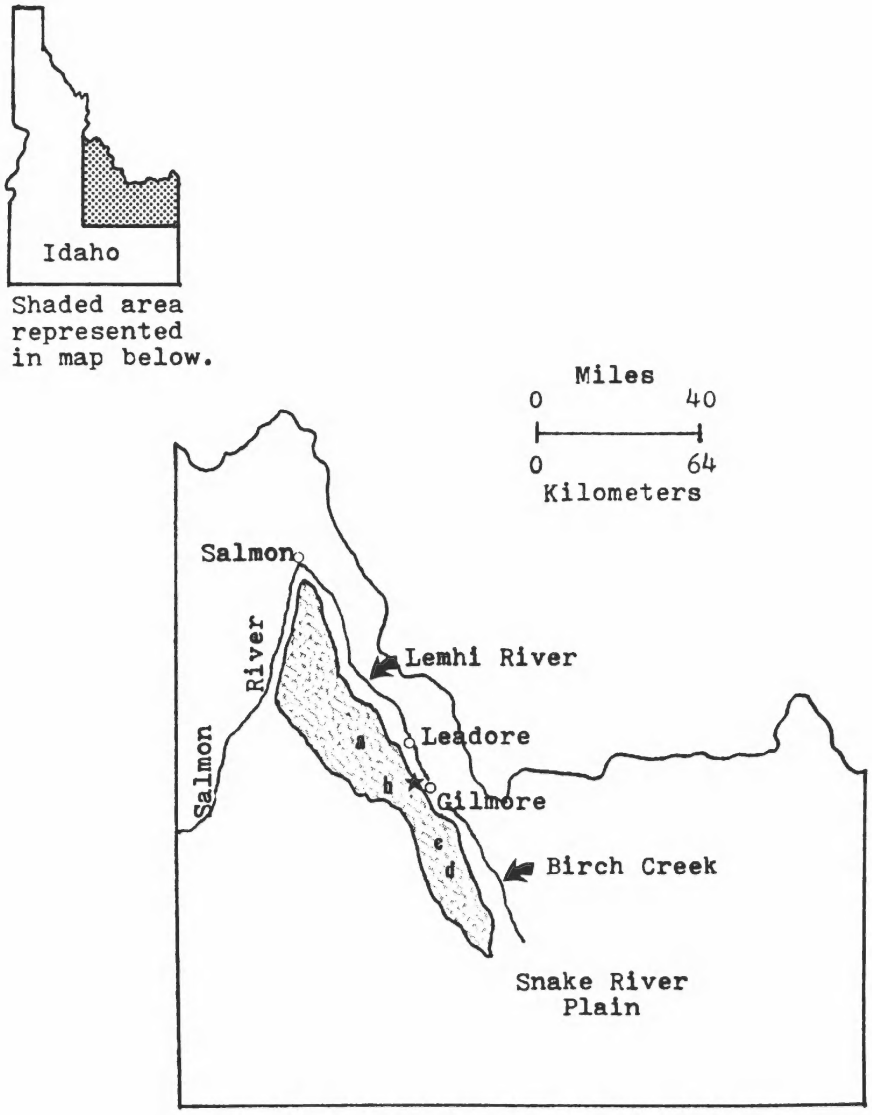

Figure 1. Location of the study area in Idaho. Shaded area in lower map represents the Lemhi Mountains. The star marks the location of the Hilltop Valley. Letters refer to major peaks in the Lemhi Mountains: a, Mogg Mountain; b, Flatiron Mountain; c, Bell Mountain; and d, Diamond Peak.

several large joints and chutes on the headwall. No faults or major structural features are shown for the valley by Hait.

Valley sidewalls are steep, in the range of 25-35°. Forest vegetation is thick on the southeastern valley sidewall. The northwestern (*i.e.*, southeastern-facing) sidewall vegetation reflects more xeric conditions, with a more open forest cover, sagebrush (*Artemisia* spp.), and grasses.

Prior references to the glacial and mass wasting history of this valley are extremely

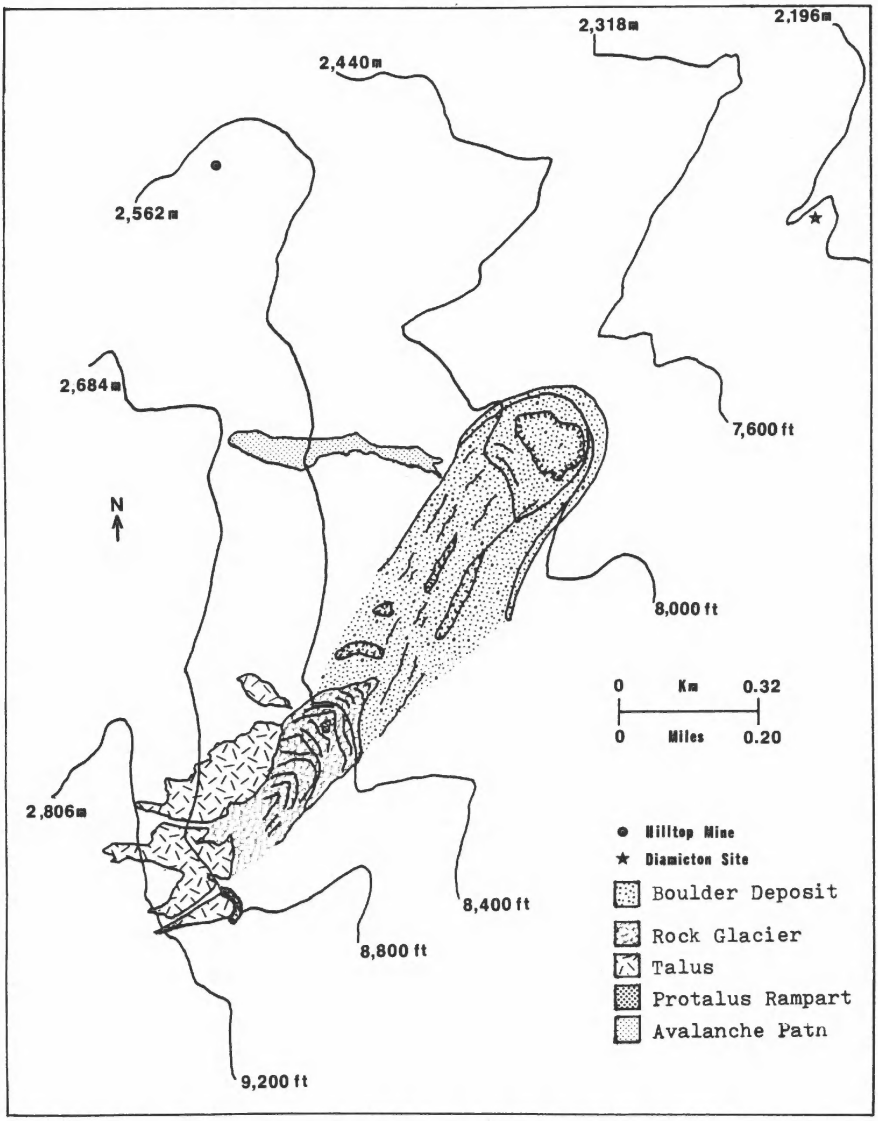

Figure 2. Generalized surficial deposits and landforms, Hilltop Valley, Lemhi Mountains, Idaho.

limited. In his preliminary aerial-photo reconnaissance, Dort (1962) classified the terminal ridge of the Hilltop Valley as "Pinedale moraine," and identified "Little Ice Age and Temple Lake deposits" on the valley floor just below the headwall. The U.S. Forest Service (1965) classified the entire valley as a "glacial trough land." The present study examines the deposits of this valley and describes the late Quaternary chronology of their development. Paleoenvironmental implications of this chronology are also presented.

The valley was chosen for two major reasons: 1) it is close to one of the four valleys studied by Knoll (1977), providing a basis for comparison of results; and 2) its apparent limited level of glaciation suggested that little destruction of deposits from earlier cold episodes had taken place (Dort 1977, iii).

Methodology

In order to determine the chronology of development of landforms attributable to late Quaternary cold episodes, it was first necessary to map their distribution and determine their origins. Field mapping of the landforms and close examinations of their surficial morphology accomplished these goals. Vertical exposures of diamictons were also studied in the field, where available. Data for several relative-age dating (RD) characteristics were also recorded at locations on the surface of the landforms in question. The distribution and origins of the mapped landforms and diamictons are presented in following sections. These discussions include age assignments and development of the late Quaternary chronology of mass wasting and paleoenvironmental change as determined from the mapped landforms (and diamictons) and their RD characteristics.

Description of the Hilltop Valley Boulder Deposit

The major depositional feature located in the Hilltop Valley is a large boulder deposit (Fig. 2). The deposit is a boulder-strewn, unstable mass of ridges, furrows, and large depressions contained behind a massive terminal (80 m high) and lateral ridge (65-70 m high) complex (the ridge referred to as Pinedale moraine by Dort (1962)). The average gradient on the surface of the boulder deposit is 233 m/km. This boulder deposit is interpreted as the remnant of an ice-cored rock glacier (Butler 1982), rather than as Pinedale moraine. It will be referred to as a boulder deposit to avoid confusion with a smaller rock glacier upvalley.

The crest of the terminal ridge of the boulder deposit is the most stable portion of the entire feature. The crestal width ranges from 4-6 m. Lithology (100% Kinnikinic quartzite), stability (relatively firm), and vegetation cover are uniform along the crest of the terminal and lateral ridge complex. Vegetation is a mature, open forest of Douglas-fir *(Pseudotsuga menziesii)* with trunks 1 m in diameter, and 25-30 m tall. Little understory exists, except for low *Juniperus* spp. bushes. Duff is thick in areas of heavier Douglas-fir coverage. Soil development along the crest of the terminal/lateral ridge complex is surprisingly poor. Two excavations on the crest revealed profiles that had, at best, an A2/C profile, with an A2 horizon of no more than a few centimeters depth. At one site on the eastern lateral ridge, the profile did not even exhibit a true A horizon. Rather, the profile had, in the strict sense, an 01/02/C sequence. Duff content in the 0 horizons was emphasized by an organic matter content (determined by loss on ignition) of 66 percent.

A major depression exists within the boulder deposit just upvalley from the 80 m-high terminal ridge (Fig. 2). This depression is 30 m deep. The slopes leading into it are unstable and steep, with slope angles of 30° the norm.

The main body of the Hilltop Valley boulder deposit is a mass of jumbled boulders strewn about with little apparent pattern. The debris is coarse and subangular, with a pronounced lack of fines, except in low-lying areas or zones with low slope angles. Rocks in the deposit are large, ranging up to several meters on the a-axis. The deposit has an extremely high porosity attributable in part to the loose packing of the clasts. Lithology of the deposit is 100 percent Kinnikinic quartzite (based on counts of 100 boulders each at five different locations on the deposit).

In addition to the large depression immediately upvalley of the terminal ridge of the deposit, many more furrows (linear depressions) and rounded depressions occur on the surface. Many longitudinal furrows exist on the surface of the deposit, with only two transverse furrows. Ridges occur in the inter-furrow areas. The depth of the furrows (measured from the crest of surrounding ridges) ranges from 2 to 10 m. Some furrows have served as collection areas for fine sediments, and as such, support a vegetation cover, whereas the slopes of others are so steep as to preclude vegetation entirely.

Where vegetation exists on the surface of the boulder deposit, it is the same as that which occupies the crest of the terminal ridge, namely Douglas-fir trees and juniper bushes. Distribution of vegetation in furrow areas was commented on above. In general, ridge crests within the main body of the boulder deposit are stable and support some concentration of Douglas firs and/or junipers.

The Hilltop Valley Rock Glacier

Progressing upvalley from the Hilltop Valley boulder deposit, the next feature encountered is a much smaller, inactive rock glacier (probably formerly ice-cemented). The toe of the rock glacier is located at approximately 2550 m elevation. One hundred-twenty meters higher is the head of the rock glacier at the base of the amphitheater walls that form the head of the Hilltop Valley, a distance of 300 m (Fig. 2).

The toe of the rock glacier rises steeply above the Hilltop Valley boulder deposit at sharp slopes angles of 35-38°. There is an abrupt transition from the boulder deposit to the rock glacier, with a significant topographic rise of 5-8 m.

The rock glacier has surficial morphology typical for such a feature. Several tranverse ridges and furrows that assist in recognizing rock glaciers occur on the surface of the Hilltop Valley rock glacier. Toward the southeastern down-valley end of the rock glacier, there is a hint of a longitudinal furrow, a characteristic also common to rock glaciers. Relative relief from the surface of the rock glacier to the bottom of the furrows varies, but is generally 3-4 m. The furrows range from 2-10 m in width. Ridge crests are up to 5 m wide.

Clasts on the surface of the rock glacier vary in size from less than 5 cm to over 1 m on the a-axis. Lithology, as determined by random counts of 30 rocks each at 5 locations, is 100 percent Kinnikinic quartzite.

Fine sediments have collected in the bottom of several of the furrow depressions. No soil is present on inter-furrow slopes or ridge crests, where unstable clasts and large interstices have prevented the accumulation of fines.

It is only within the furrow depressions that surface vegetation occurs on the rock

glacier. Small subalpine fir *(Abies lasiocarpa)* trees, low bushes, and alpine flowers are concentrated in these limited areas. Some small stabilizing patches of low bushes are also located on peripheries of the rock glacier and on low-angle slopes just above the bases of some of the transverse furrows.

One major transverse furrow divides the rock glacier into two distinct topographical components or lobes. This major furrow is 5 m deep and averages 10 m wide.

There is no distinct pit at the head of the rock glacier, a feature that characterizes some rock glaciers (Luckman and Crockett 1978). The rock glacier is contiguous with, and over-ridden by, surrounding talus slopes at the base of the valley headwall and northwestern sidewall. These characteristics suggest that the rock glacier was formerly ice-cemented, rather than ice-cored.

The Hilltop Valley Talus and Protalus Deposits

Talus deposits and protalus features are common in the central Lemhi Range (Knoll 1977). The Hilltop Valley is no exception, with talus covering the base of the valley headwall. A protalus deposit is located below the valley headwall and above the rock glacier.

The protalus deposit on the slope below the valley headwall is a protalus rampart. The rampart is approximately 80 m long, 2 m high, and 3 m wide; it is curved in plan view (Fig. 2). This form of protalus is what Knoll (1977) defined as a protalus loop rampart, subclass single loop.

Field examination of the protalus rampart revealed a coarse, bouldery, unstable landform with virtually no soil development along the rampart crest. Fines have accumulated at the base of the proximal slope of the rampart, allowing establishment of small (4-5 m high) subalpine fir trees. Lithology of the rampart is 100 percent Kinnikinic quartzite.

Talus covers the base of the headwall of the Hilltop Valley and accumulates in positions along the sides of the valley headwall. Morphologically the talus accumulates as cones and sheets, indicative of rockfall, rather than avalanche, origins (according to White (1967)).

The Hilltop Valley talus deposits consist of coarse blocks deposited with few fines. These characteristics also imply a rockfall origin (White 1967). Dead wood is located at the bases of some of the talus sheets, particularly on the northwest side of the headwall, suggesting that snow avalanches pass over the surface of the talus (from snow accumlated in chutes in the valley walls) and transports vegetative materials, but with little apparent geomorphic alteration.

The talus deposits may be divided into two main groups (one of which is shown in Table 2), on the basis of stability, vegetative cover, and percentage lichen cover. The first group, with up to 10 percent lichen cover and some vegetative development (small juniper bushes and subalpine fir), are barely stable to unstable, whereas the second group is extremely unstable, geomorphologically active, and lacking in vegetation or significant lichen cover.

Talus at the base of the valley headwall and northwestern sidewall over-rides the head and side of the rock glacier on the valley floor. A boulder ridge extends from the base of the northwestern sidewall talus toward, and merging into, the rock glacier. This ridge is also being over-ridden by fresh talus on the end at the base of the sidewall.

TABLE 2. Relative-age data for surficial deposits within the Hilltop Valley.

Deposit/ Landform	Vertical Relief	Distal Slope Angle	Minimum Age as Determined through Tree-Ring Analysis	% Boulders Implanted (a)	Average Degree of Implantation (b)	% Lichen Cover	Stability of Footing
Boulder Deposit	60-80 m	33°	450 years	Ranges from 0% to 100%	Ranges from 10% to 90%	80-95%	Ranges from firm on terminal ridge to unstable within body of deposit.
Ice-cemented Rock Glacier	Varies, 8 m at toe	35-38°	No Data	Less than 20%	0% on surface 10-20% in furrows	60-70%	Barely stable in furrows, barely stable to unstable on surface.
Protalus Rampart	30-200 cm, highest on distal side	Not applicable for dating purposes	No Data	0%	0%	30-45%	Unstable to very unstable and treacherous.
Talus Deposits	Not applicable	Not applicable	No trees present	0%	0%	0% on active talus, up to 10% on recently inactive talus	Very unstable and treacherous, constantly moving underfoot.

(a) an estimation of how many boulders, in %, were at least partially implanted in a 2m x 3m transect on the surface of the deposit.

(b) determined by excavation of ten boulders greater than 0.3 m in diameter on the surface of the deposit.

Hilltop Valley Snow Avalanche Paths

As noted in the description of talus slopes above, snow avalanches occur on the walls surrounding the head of the Hilltop Valley. One other avalanche path is also located on a slope above the Hilltop Valley boulder deposit (Fig. 2).

Snow avalanches that occur within this avalanche path have cut a distinct swath through the mature Douglas fir forest on the northwestern valley sidewall. The path descends from an elevation of 2684 m to 2538 m. Vegetative conditions within the avalanche path attest to frequent avalanching, perhaps as often as every one to two years (Schaerer 1972).

Chronology of Development of Hilltop Valley Surficial Deposits

A lack of materials suitable for radiocarbon dating within the Hilltop Valley necessitated the use of RD techniques in order to establish periods of deposition or cessation of activity.

Figure 3 summarizes the age assignments of the surficial deposits/landforms in the Hilltop Valley based on the RD data presented in Table 2. A trend of decreasing areal coverage as the present is approached is apparent, a conclusion similar to one reached for surficial deposits in an adjacent valley (Butler 1982). This conclusion in turn implies a trend of decreasing severity of successive cold climatic episodes as the present is approached. The one exception to this conclusion would apparently be the areal extent of Audubon-aged deposits. However, it is likely that the talus deposits attributable to the Arapaho Peak stade have masked evidence of deposits assigned earlier ages, including deposits of Audubon age.

The Hilltop Valley boulder deposit RD characteristics suggest cessation of activity in the early Holocene. The ice cored rock glacier probably developed, however, during the last stade of Pinedale glaciation. Ice-cored rock glaciers are relatively insensitive to climatic changes due to their insulating cover of rubble (Luckman and Osborn 1979), so it is probable that stagnation of the late Pinedale Hilltop Valley rock glacier did not occur until the early Holocene, accounting for the boulder deposit's RD characteristics.

Acceptance of an ice-cemented origin for the smaller rock glacier in the valley permits direct correlation of the rock glacier development with local or regional climatic effects (*i.e.*, the Triple Lakes stade of Neoglaciation (Luckman and Osborn, 1979)). RD characteristics did not distinguish between the two lobes of this smaller rock glacier. However, the fact that two lobes and a large intervening transverse furrow exist on the surface of the rock glacier suggests two periods of movement. The second period of movement (represented by the upper lobe) did not entirely over-ride the lower lobe, implying: either 1) that the lower portion of the rock glacier formed during a more severe climatic period of the Triple Lakes stade than that which resulted in the upper, over-riding, lobe; or 2) inadequate material at the valley head during the period of the second advance prevented a complete over-ride of the lower lobe. Either interpretation accepts the division of the Triple Lakes period into two substades.

Diamicton Exposures Adjacent to the Hilltop Valley

The major geomorphic features within, and on the surrounding slopes of, the Hilltop Valley have been described. However, diamicton exposures of interest, which may shed light on late Quaternary paleo-environmental conditions, exist in immediately adjacent

areas. These exposures and paleoclimatic inferences drawn from them are presented below.

Hilltop Valley Diamicton Site

A bouldery diamicton is exposed in a cut located 750 m beyond the terminal ridge of the Hilltop Valley boulder deposit (Fig. 2). The exposure is rich in quartzite boulders

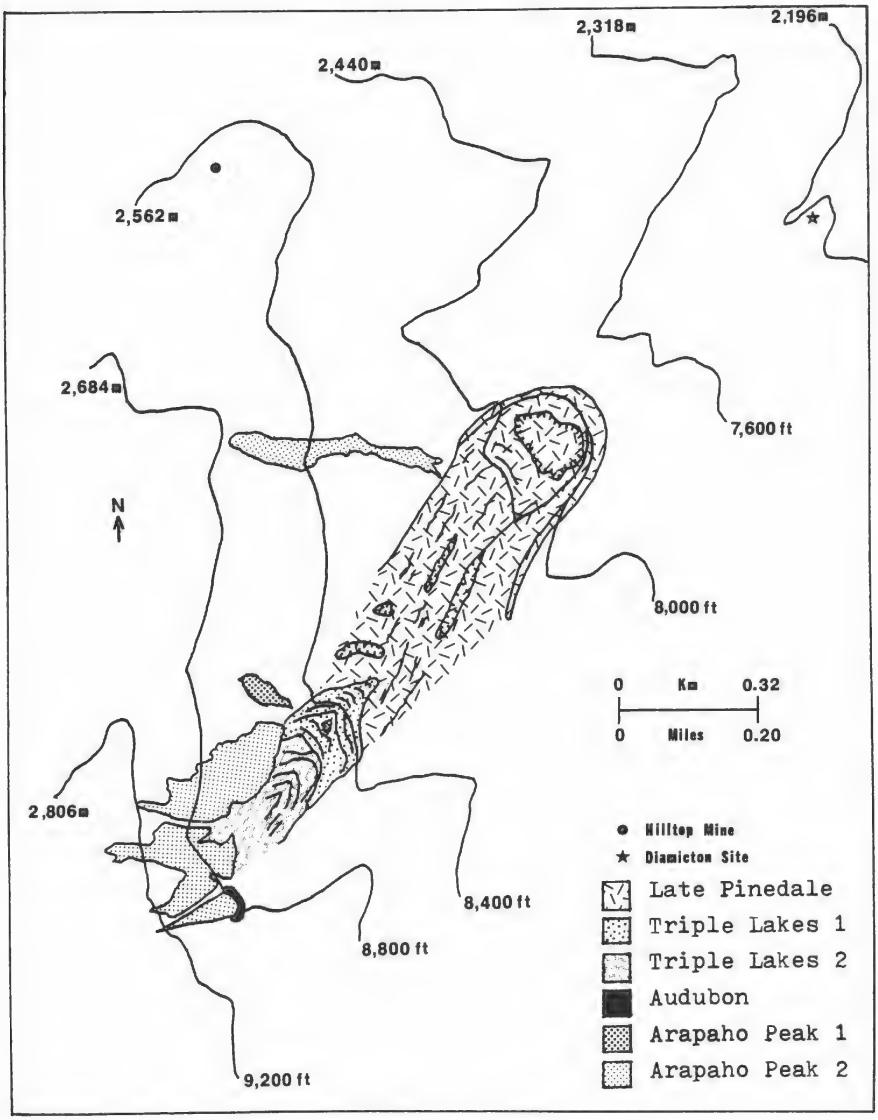

Figure 3. Age assignments of surficial deposits and landforms, Hilltop Valley, Lemhi Mountains, Idaho.

that often have thick white carbonate coatings on their undersides. There is no surficial expression or landform associated with the diamicton deposit.

The Kinnikinic quartzite lithology of the deposit supports a possible glacial origin. However, other processes which would adequately transport quartzite boulders to this location (such as massive landslides, sturzstroms, or rock glaciers) cannot be ruled out.

The thickness of carbonate coatings on the quartzite clasts suggests an old, pre-Bull Lake age for the diamicton. The smoothing of any former surficial expression of the deposit also suggests antiquity. A lack of datable material in the exposure prevents any definite placement of the deposit within a late Quaternary framework.

If the diamicton is attributable to glaciation, the location of the deposit well beyond terminal moraines would not be unusual in the Lemhi Range. Pre-Bull Lake erratics attributed to glaciation (identified by Knoll (1977)) extended much farther from the mountain front than the Hilltop Valley diamicton. Although no firm conclusions can be drawn from the diamicton, it is at least suggestive of pre-Pinedale and Bull Lake glaciation originating in the Hilltop Valley.

Hilltop Mine Site

An interesting stratigraphic sequence is exhibited in a bulldozer exposure adjacent to the Hilltop Mine on a spur of Portland Mountain (Fig. 2). The exposure is approximately 30 m long, and the units revealed extend the entire length of the cut. The slope into which the exposure was bulldozed is steep (27°).

A poorly-developed surface soil up to 15 cm in thickness overlies a diamicton layer consisting of elongated, subrounded, and crudely imbricated pebbles. This layer is 46 m thick and lies at an angle of 29°. The imbricated pebbles provide the unit with the illusion of motion, as if it were slowly moving, perhaps sliding, downslope.

Beneath the imbricated diamicton is a paleosol 5 cm thick; it is powdery and strongly carbonate in nature. Fine purplish-tinted rootlets are concentrated within the paleosol unit.

Under the powdery paleosol is another, even more crudely imbricated pebble unit 11-13 cm thick. The imbrication is more poorly developed and/or preserved than in the unit above the paleosol.

The strong-sloped appearance of both units of imbricated pebbles suggests some sort of periglacial downslope transport or creep, as if an entire unit of rocks had slid downslope over a frozen base. The sloped imbrication is certainly more suggestive of downslope sliding over a frozen surface than mere colluvial creep.

The paleosol in the exposure is strikingly similar to a Pinedale/Bull Lake paleosol described from a number of locations in an adjacent valley (Butler 1982). If the Hilltop Mine paleosol is correlative with that paleosol, as their physical characteristics suggest, the imbricated pebbles overlying the paleosol could be attributed to periglacial downslope creep/sliding during some portion of Pinedale time and the lower imbricated unit to a similar process during the Bull Lake period. With widespread glaciation in the Lemhi Range during Pinedale and Bull Lake times, it is probable that permafrost existed at higher elevations such as the Hilltop Mine Site.

Conclusions

The accuracy of the chronological assignments of deposits within the Hilltop Valley is

considered good, given the constraints of RD data. Accuracy of time assignments in periods earlier than the mid-Holocene is more questionable.

The lack of hard evidence for glaciation in the Hilltop Valley during the Holocene is one important feature of the chronology; another is the apparent lessening severity of Neoglacial stades as the present is approached. Decreasing severity is a trend common in many areas of the central Rocky Mountains (Benedict 1981).

The chronology for the Hilltop Valley and surrounding sites is simpler than the composite chronology developed by Knoll (1977). Even though the Hilltop Valley chronology is less complicated than that derived by Knoll, certain similarities between the two are apparent. For example, both chronologies share a similar pattern during the Neoglacial, although the geomorphic responses to the cold climatic conditions of that period varied somewhat. Two periods of Triple Lakes activity were apparent in the Hilltop Valley, whereas only one glacial period was identified in an adjacent glaciated valley to the south (Butler 1982). It is possible that the presumably milder climate of the Hilltop Valley could not support continuous periglacial conditions and resultant rock glacier development during the Triple Lakes period. Protected and favorably oriented valleys in the Lemhi Mountains may have been able to sustain one complete period of glaciation stretching through the time covered by two periods of rock glacial activity in the Hilltop Valley (and Colorado Front Range; Benedict (1981)). The Audubon and Arapaho Peak stades in the Hilltop Valley and Knoll's valleys produced climatic conditions and geomorphic responses of striking similarity.

Little is known about the Pleistocene climatic events and geomorphic responses in the Hilltop Valley, athough diamicton deposits are suggestive of a complex history. More events probably occurred in that valley than show up in the geomorphic record, but how such hypothetical events would match with those described by Knoll (1977) is not known. Presumably, the events in the valleys would match well, such as occurs with the record of the adjacent glaciated valley and the study valleys several kilometers to the south described by Knoll. Late Quaternary climatic episodes and changes were evidently regional in nature in the Lemhi Mountains, although the form and intensity of geomorphic and paleoenvironmental responses varied within individual valleys.

Acknowledgments

Dr. Wakefield Dort, Jr., first brought the unusual deposits of the Hilltop Valley to my attention and suggested that a detailed study of them would be fruitful. The work described in this paper formed a portion of a doctoral dissertation under the supervision of Dr. Curtis J. Sorenson. I would like to thank the Geological Society of America (Research Grant 2587-80) and the University of Kansas Graduate School for financial support; the U.S. Forest Service for assistance during my work in the Lemhi Mountains; Drs. Curtis J. Sorenson, Wakefield Dort, Jr., and William C. Johnson for advice in the field; J. Butler, M. Butler, B. Hall, K. Millington, & R. Sewell for assistance in the field; and Mr. Jim Ellsworth & Mr. Sandy Simms for access across their lands.

Literature Cited

Benedict, J. B. 1981. *The Fourth of July Valley: Glacial Geology and Archeology of the Timberline Ecotone.* Research Report No. 2, Center for Mountain Archeology, Ward, Colorado.

Butler, D. R. 1982. *Late Quaternary Glaciation and Paleoenvironmental Changes in Adjacent Valleys, Lemhi Mountains, Idaho.* Unpub. Ph.D. thesis, Univ. of Kansas.

Dort, W. Jr. 1962. Multiple glaciation of southern Lemhi Mountains, Idaho: preliminary reconnaissance report. *Tebiwa* 5: 2-17.
———. 1977. Foreword, *in*: Chronology of Alpine Glacier Stillstands, East-Central Lemhi Range, Idaho, by Kenneth M. Knoll, Idaho State Univ. Museum of Natural History, Pocatello.
Hait, M. H., Jr. 1965. *Structure of the Gilmore Area, Lemhi Range, Idaho*. Unpub. Ph.D. thesis, Pennsylvania State Univ.
Knoll, K. 1977. *Chronology of Alpine Glacier Stillstands, East-Central Lemhi Range, Idaho*. Special Publication, Idaho State Museum of Natural History, Pocatello.
Luckman, B. H., and K. J. Crockett. 1978. Distribution and characteristics of rock glaciers in the southern part of Jasper National Park, Alberta. *Canadian Journal of Earth Sciences* 15: 540-550.
———, and G. D. Osborn. 1979. Holocene glacier fluctuations in the middle Canadian Rocky Mountains. *Quaternary Research* 11: 52-77.
Madole, R. F. 1980. Time of Pinedale deglaciation in north-central Colorado: further considerations. *Geology* 8: 118-122.
Pierce, K. L., J. D. Obradovich, and I. Friedman, 1976. Obsidian hydration dating and correlation of Bull Lake and Pinedale Glaciations near West Yellowstone, Montana. *Geological Society of America Bulletin* 87: 703-710.
Richmond, G. M. 1965. Glaciation of the Rocky Mountains *in*: The Quaternary of the United States, (H. E. Wright, Jr., and D. G. Frey, eds.), Princeton Univ., Princeton.
Ruppel, E. T., and M. H. Hait, Jr. 1961. Pleistocene geology of the central part of the Lemhi Range, Idaho. *U.S.G.S. Professional Paper* 424-B.
Schaerer, P. A. 1972. Terrain and vegetation of snow avalanche sites at Rogers Pass, British Columbia, *in*: Mountain Geomorphology, (O. Slaymaker and H. J. McPherson, eds.), Tantalus Research Ltd., Vancouver.
U.S. Forest Service. 1965. *Land Type Association Map*, Salmon National Forest, Idaho. U.S. Forest Service, Ogden, Utah.
White, S. E. 1967. Rockfall, alluvial, and avalanche talus in the Colorado Front Range. *Geological Society of America Special Paper No. 115.*
Winter, M. H. 1982. Upper treeline fluctuation in the Lemhi Range, southeastern Idaho. *AAG Program Abstracts*, Association of American Geographers 78th Annual Meeting, San Antonio, Texas.

Received August 10, 1982
Accepted for publication August 26, 1982

Ronald J. Kendall[1]

Gary W. Norman[2]

and

Patrick F. Scanlon

Department of Fisheries and Wildlife Sciences
Virginia Polytechnic Institute
and State University
Blacksburg, Virginia 24601

Lead Concentrations in Ruffed Grouse Collected from Southwestern Virginia

Abstract

Sixteen Ruffed Grouse (*Bonasa umbellus*) were collected from mountainous areas in southwestern Virginia by shooting and their livers and tarsometatarsal bones analyzed for lead (μg lead/g, d.w) by atomic absorption spectrophotometry. Liver lead concentrations averaged ($\pm$S.E.) 2.27$\pm$0.43 μg/g, and no evidence of ingested lead shot was found. Overall, mean ($\pm$S.E.) lead concentration in bones was 2.78$\pm$0.57 μg/g, and values ranged from 0.44-9.15μg/g. Bone lead concentrations of Ruffed Grouse appear to provide reasonably realistic background values for lead in remote forested areas in Virginia.

Introduction

Lead contamination is a continuing problem for populations of wild avian species either from ingestion of spent lead shot (Bellrose 1959, Westemeier 1966, Lewis and Legler 1968, Kendall and Scanlon 1979) or from exposure to environmental lead contamination (Tansy and Roth 1970, Siegfried *et al.* 1972, Ohi *et al.* 1974, Kendall and Scanlon 1979). There is a paucity of information on background concentrations of lead in avian species collected from relatively undisturbed habitats. Data from such species should better approach "normal" background tissue lead concentrations and thus be useful in evaluation of elevated concentrations. This report is concerned with lead concentrations in Ruffed Grouse (*Bonasa umbellus*), a nonmigratory species inhabiting relatively remote habitats in southwestern Virginia. Scanlon *et al.* (1980) have addressed concentrations of lead and other heavy metals in feathers of Ruffed Grouse; this study addresses lead concentration in livers and skeletal tissue of Ruffed Grouse.

Methods and Materials

Sixteen Ruffed Grouse were collected by shotgun from mountainous areas in southwestern Virginia. Each bird was transferred to the laboratory, where the liver and tarsometatarsal bone were dissected free and frozen for later lead analysis. Tissues from individual birds were dried, ashed, and dissolved in acid. The concentration of lead was determined by atomic absorption spectrophotometry using an Instrumentation Labora-

[1]Present address: Huxley College of Environmental Studies, Western Washington University, Bellingham, Washington 98225.

[2]Present address: West Virginia Wildlife Resources Division, Point Pleasant, West Virginia 25550.

tories Model 351 spectrophotometer in the flame mode. Procedures used in preparing samples and in determining heavy metal concentrations are given in Scanlon *et al.* (1980b). Concentrations of lead were calculated in terms of $\mu g/g$ dry weight (d.w.) in both the liver and tarsometatarsal bone.

Results and Discussion

Overall mean ($\pm$S.E.) lead concentration in tarsometatarsal bones of Ruffed Grouse was 2.78 ± 0.57 $\mu g/g$, and values ranged from 0.44-9.15 $\mu g/g$ (Fig. 1). These lead

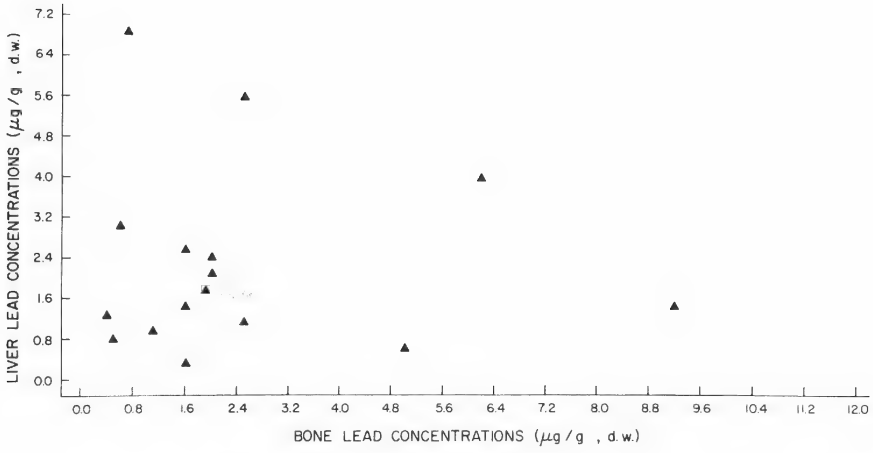

Figure 1. A plot of bone lead and liver lead concentration ($\mu g/g$, d.w.) in Ruffed Grouse collected from southwestern Virginia.

concentrations in skeletal tissue were considerably below those found in Mourning Doves (*Zenaida macroura*; range of 1.02-763.65 $\mu g/g$ bone lead; $N = 412$) (Kendall and Scanlon 1979) and Rock Doves (*Columba livia*; range of 6.63-727.86 $\mu g/g$ bone lead; $N = 39$) (Kendall and Scanlon 1982), although lead in their femurs was determined. Mourning Doves had a mean ($\pm$S.E.) bone lead concentration of 43.07 $\pm$ 4.44 $\mu g/g$ in their femurs and represent a species that often inhabits areas of high human population densities with consequent potential for increased exposure to environmental lead (Kendall and Scanlon 1979). In contrast, the Ruffed Grouse is a species occupying more remote, and presumably more pristine, environments. The lead concentrations in tarsometatarsal bone approximate values published for Ruffed Grouse features (Scanlon *et al.* 1980a).

Overall mean (±S.E.) lead concentration in livers of Ruffed Grouse was 2.27 ±0.43 μg/g. No evidence of ingested lead shot was found, as liver lead concentrations were relatively low in grouse when compared with liver lead concentrations ($X \pm S.E. = 11.4 \pm 3.6$ μg/g) in Japanese Quail (*Coturnix coturnix japonica*) that had ingested one No. 8 lead pellet (Kendall and Scanlon 1981). Mourning Doves had liver lead concentrations that ranged from undetectable up to 76.45 μg/g ($N = 412$) in birds that had ingested lead shot. However, liver lead averaged 2.94 μg/g (d.w.) in doves, slightly higher than in grouse (Kendall and Scanlon 1979). Although Ruffed Grouse and Mourning Doves were collected by shooting, contamination of liver tissue by penetrating lead pellets could be a possibility. However, such lead contamination of livers is unlikely, as Japanese Quail shot through the liver with lead pellets did not have higher liver lead concentrations than those decapitated (Kendall and Scanlon 1981).

Bone lead concentrations of Ruffed Grouse appear to provide reasonably realistic background values for lead in remote forested areas in southwest Virginia. The values for liver lead concentrations appear to be less sensitive in contrasting a remote dwelling avian species, such as the Ruffed Grouse, with a species probably exposed to greater amounts of environmental lead, such as the Mourning Dove. However, liver lead concentrations can provide valuable information on the possible ingestion of spent lead shot by Ruffed Grouse. It appears that Ruffed Grouse collected by hunters are a useful source of tissues for monitoring lead concentration in avian species that inhabit relatively remote ecosystems.

Literature Cited

Bellrose, F. C. 1959. Lead poisoning as a mortality factor in waterfowl populations. Ill. Nat. Hist. Surv. Bull. 27(3):235-288.

Kendall, R. J., and P. F. Scanlon. 1979. Lead concentrations in Mourning Doves collected from middle Atlantic game management areas. Proc. Ann. Conf. S.E. Assoc. Fish and Wildl. Agencies 33:165-172.

———, and ———. 1981. Tissue lead concentrations in Japanese Quail ingesting lead pellets or shot with lead pellets. Bull. Environ. Contam. Toxicol. 26:652-655.

———, and ———. 1982. Tissue lead concentrations and blood characteristics of Rock Doves (*Columba livia*) from an urban setting in Virginia. Arch. Environ. Contam. Toxicol. 11: 265-268.

Lewis, J. C., and E. Legler, Jr. 1968. Lead shot ingestion by Mourning Doves. J. Wildl. Manage. 32(3):476-482.

Ohi, G., H. Seki, K. Akiyama, and H. Yagyu. 1974. The Pigeon, a sensor of lead pollution. Bull. Environ. Contam. Toxicol. 12:92-98.

Scanlon, P. F., R. G. Oderwald, T. J. Dietrick, and J. L. Coggin. 1980a. Heavy metal concentrations in feathers of Ruffed Grouse shot by Virginia hunters. Bull. Environ. Contam. Toxicol. 25: 947-949.

———, V. D. Stotts, R. G. Oderwald, T. J. Dietrick, and R. J. Kendall. 1980b. Lead concentrations in livers of Maryland waterfowl with and without ingested lead shot present in gizzards. Bull. Environ. Contam. Toxicol. 25:855-890.

Siegfried, W. R., P. G. H. Frost, E. P. Redelinghuys, and R. P. Van der Mere. 1972. Lead concentrations in the bones of city and country doves. South African J. Sci. 68(9):229-230.

Tansy, M. F., and R. P. Roth. 1970. Pigeons: a new role in air pollution. J. Air Pollut. Cont. Assoc. 20(5):307-309.
Westemeier, R. L. 1966. Apparent lead poisoning in a wild Bobwhite. Wilson Bull. 78:471-472.

Received April 29, 1982
Accepted for publication June 18, 1982

Richard G. Holloway

Biology Department
Texas A&M University
College Station, Texas 77843

Analysis of Surface Pollen from Alberta, Canada, by Polar Ordination

Abstract

Surface pollen assemblages from 29 vegetational stands located throughout the Province of Alberta were analyzed using polar ordination and were then compared to vegetational data analyzed using the same techniques. The results revealed that a correlation between these sets of data does exist. By using the techniques of polar ordination, the surface pollen assemblages of the 29 stands clustered into five groups which were representative not of the vegetational composition of the stand, but of the dominant vegetational association in that area. These results suggest that polar ordination is a promising analytical technique that may be particularly useful in delimiting fossil pollen assemblages.

Introduction

Pollen analysts have long been interested in the relationships that exist between the vegetational composition of a plant community and its constituent pollen rain. Previous investigators approached this problem by a variety of methodological procedures, including the analyses of surface moss polsters (Hansen 1946, King and Kapp 1963, McAndrews and Wright 1969, Mack and Bryant 1974, Heusser 1977) and pollen traps (Rowley 1955). More recently, Webb and McAndrews (1976) have used trend surface analysis to map the distribution of the pollen rain across broad vegetational zones in Canada. These data have proven invaluable as an aid in the interpretation of fossil pollen chronologies, but, unfortunately, the basis for many of these studies are geographically restricted.

The palynological record from Alberta is only poorly known from a few selected sites located principally in the central part of the province (Hansen 1949a, 1949b; Lichti-Federovich 1970, 1972; Jackson 1979; Kroker 1979; Holloway *et al.* 1981). However, in order to precisely interpret these palynological records, it is necessary to first understand the existing relationships between the vegetation and the surface pollen rain from this region.

Janssen (1970) has correctly observed that the pollen rain of any particular plant community is comprised not only of the pollen rain produced locally, but in addition, contains pollen deposited as a result of long distance transport from adjacent communities in the paths of prevailing winds. Thus, in attempting to interpret the distribution of the major pollen rain, it is necessary to view the spatial distribution of major plant associations throughout the region. Since vegetational patterns and the distribution of extant plant communities can be easily investigated by using the gradient analysis approach (Whittaker 1967), I decided to apply this methodology to analyses of surface pollen data collected from communities located throughout the Province of Alberta (Fig. 1).

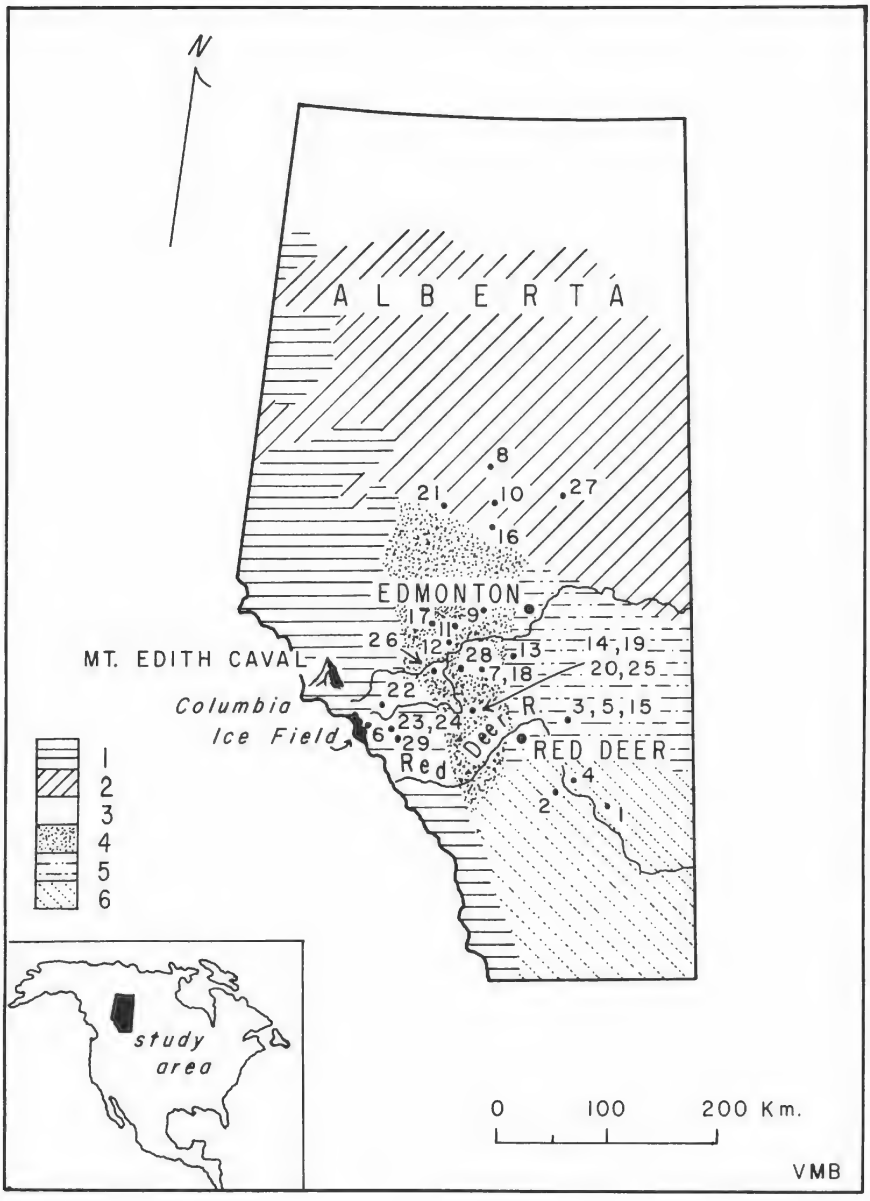

Figure 1. Map of Alberta, Canada, showing sampling locations and major vegetational associations. 1=Montane and Foothills region; 2=Mixedwood Forest Region; 3=Northern Mixedwood Forest Region; 4=Spruce-Aspen Ecotone; 5=Aspen Parkland; 6=Grasslands. Vegetational associations are generalized after Rowe (1972) and North (1976).

Methods and Materials

The vegetational composition of 29 plant communities, which represent the major plant associations of Alberta (North 1976), were studied using the releve method of Muller-Dombois and Ellenberg (1974). This method allowed for the statistical analysis of data recovered from several stands of each plant association. A 10 X 10 m plot from each stand was used throughout, irrespective of the vegetational composition of the stand, in order to provide a more nearly accurate comparison between stands (Muller-Dombois and Ellenberg 1974). The vegetation of each plot was described by vertical stratification levels consisting of canopy, secondary canopy, tall shrub, low shrub, herb and grass. Space limitations prevent the inclusion of the raw vegetational data. These data may be obtained by corresponding with the author. The relative abundance of each species was determined separately for each stratigraphic level by Daubenmire's (1974) percent cover estimates, and all species identifications were based on Moss (1974). Modern surface pollen samples were collected from each stand using the "pinch" method of Adams and Mehringer (1975). Each composite pollen sample consisted of 25 sub-samples.

The pollen samples were prepared for microscopic analysis following the method of Faegri and Iversen (1975). Small sub-samples of the surface "pinch" samples collected from each stand were first treated with 10 percent NaOH and screened through 200 μm screen. The residue was acetylated (Erdtman 1960). After dehydration, the concentrated pollen residues were transferred to a mounting medium of 1000 cs silicon oil prior to routine examination at 430X magnification. Horizontal transcects of 1 mm intervals were used throughout, and the entire slide was scanned to avoid non-random distribution of pollen on the slide (Brooks and Thomas 1967). A minimum sum of 200 grains per sample was used throughout (Barkley 1934).

Both pollen and vegetational data were then analyzed using polar ordination. Polar ordination is defined as an arrangement of units in a uni- or multi-dimensional order (Goodall 1953 in Bray and Curtis 1957). Ordination, as further developed by Bray and Curtis (1957), is based on the selection of two samples as poles (endpoints) with all other samples positioned along an axis with reference to these endpoints. Three different measures of community similarity are available: percentage distance (PD), Euclidian distance (ED), and coefficient of community (CD). The ordination for this study used percentage distance as the measure of the computations. The endpoints were automatically selected by the Ordiflex Program (Gauch 1977) and provide for a spatial arrangement of the communities along one or more axes based on the degree of similarity between pairs of communities.

Relative pollen frequencies of the 19 most commonly occurring taxa from these samples were used (Table 1). Because of the morphological similarity of palynomorphs, identification and assignment of pollen morphological types to taxonomic categories (except in rare instances) require the use of more inclusive taxa, such as genus or family. On the other hand, identification of the vegetational composition of such stands is usually to the species or sub-species taxonomic level. In the past, studies such as these have computed the vegetational composition and pollen directly, regardless of the level of distinction of the taxonomic level (Cross *et al.* 1980, Fine 1980, Margraf *et al.* 1981). These comparisons using different taxonomic levels in the data base, have led to confusion and lack of agreement of the statistical analyses. In order to compare

TABLE 1. Pollen percentages from surface samples of 29 plant communities.

Pollen taxa	1	2	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Pinus	8	11	13	19	24	30	33	38	37	35	47	46	55	60	66	54	63	62	62	58	74	70	77	78	77	73	78	86	94
Picea	3	+	4	6	7	8	6	18	5	25	11	30	23	7	10	31	10	20	16	9	15	17	14	15	5	11	18	7	2
Abies						2				+		+		+		+	+	+	+	3		3	+			+	1		
Larix							3		+	+	+	+				+	+	2					+					+	+
Populus		3		+	3		+			+	+	+	+	+	3		4	+					+		+	2			
Betula			+	2	+	12	30	19	7		2	13	12	8	3	8	11	4	9	15	2	3	2	1	7	6		4	1
Alnus			4	3	1	21	9	10	2	4	2	6	3	12	4	2	4	2	7	6	4	4	2	2	6	6	+	2	+
Salix	3	12	12	5	3	10	5	3	7	+	3	2	3	+	+	+	+	3	2	1	1	+			2	+		+	
GRAMINEAE	20	35	20	13	51	3	2	3	2	3	7	2	3	5	6		4		1	+	3	+	+	+	1	+			
Cheno-am	13	7	2	7	12	+	+		+	+	+		+	1		+	1					+				+	+		
ROSACEAE		3	+	+	+	11	4			+	+		+		+	+		4	+	+					2				+
ERICACEAE						+	2						+		3	+				4									
CRUCIFERAE			+	+	+		1		3	+	+	+				+	+	+		+									
COMPOSITAE	+		7	1	1	+	1	+	2	+	2			+	1	+	+	2		+		+	+	+	+				
LIGULIFLORAE	+		1	+	+			+	2		17		+	+	+		+				+								
Artemisia	45	12	27	25	1	+	+	+					+		+	+			+				+	+					
CYPERACEAE		+	+	2	+			+											+	+		+	+	1					
Typha			+															+		+									+
Opuntia		3																											
Selaginella	6	8		10																									
OTHER	+	4	2	3	2	2	+	5	25	+	4	+	+	1	+	+	+	2	1	2							1		
Total grains	208	101	214	207	213	229	210	235	258	248	326	248	213	208	208	215	277	213	234	258	239	226	259	385	290	217	328	278	268

*Pollen sum=101 grains, not statistically valid.

+ = Less than 1%.

NOTE percentages calculated to nearest whole percentage.

data from similar taxonomic levels, I collapsed the precision of the vegetational data in favor of the most precise level of identification that is available from the pollen record.

Results

Ordination of the surface pollen samples from 29 releve plots provided a single dimensional ordering of these stands (Table 2). Pollen percentages of five dominant taxa (*Pinus, Picea, Betula, Alnus* and Gramineae) were then plotted in relation to the axis position of these stands as delineated by the ordination (Fig. 2). The stands were divided into five groups (G1 through G5) based on the observed distribution of these

TABLE 2. X—axis co-ordinates and group placement of stands by ordination.

Stand no.	Pollen data	Group	Vegetational data	Group
1.	0.00000	1	0.00000	A
2.	14.07146	1	3.44531	A
3.	14.97954	1	2.04519	A
4.	20.45224	1	1.43805	A
5.	40.99825	1	14.09084	B
6.	63.01531	2	62.61801	C
7.	67.86011	2	90.42969	D
8.	68.45145	2	51.05864	C
9.	69.41211	2	23.78120	B
10.	70.06535	2	44.67065	C
11.	71.74953	3	45.80246	C
12.	79.39542	3	45.21080	C
13.	80.02547	3	51.04027	C
14.	82.41209	3	38.29805	C
15.	84.05510	3	40.32820	C
16.	84.76803	3	86.06071	D
17.	85.16086	3	33.84874	C
18.	86.87184	3	60.92207	C
19.	87.17326	3	47.42842	C
20.	87.74373	3	76.25789	D
21.	89.88901	4	59.69341	C
22.	91,30963	4	20.34209	B
23.	92.39781	4	23.74863	B
24.	92.54359	4	18.25023	B
25.	92.71649	4	90.09758	D
26.	94.12788	4	51.23453	C
27.	95.00801	4	85.17970	D
28.	96.70612	5	75.71420	D
29.	99.99998	5	99.99998	D

five pollen taxa and natural breaks in the axis position. These group designations are delimited in Fig. 2 by vertical dashed lines.

As a test for the statistical significance of these groups, the mean frequency and ranges of pollen percentages were computed for each of the five dominant pollen taxa by group. A Chi-square test for the strength of this relationship was performed and yielded a Chi-square value of 222.86 with 24 degrees of freedom. This value revealed that the distribution of pollen taxa was statistically significant at least at the 0.001 level.

A second polar ordination was then performed on the vegetational data. The resulting axis positions of these stands are also presented in Table 2. Based on the natural breaks in the ordination, four groups were identified (denoted alphabetically in Table 2). In an attempt to statistically compare the degree of similarity between the vegeta-

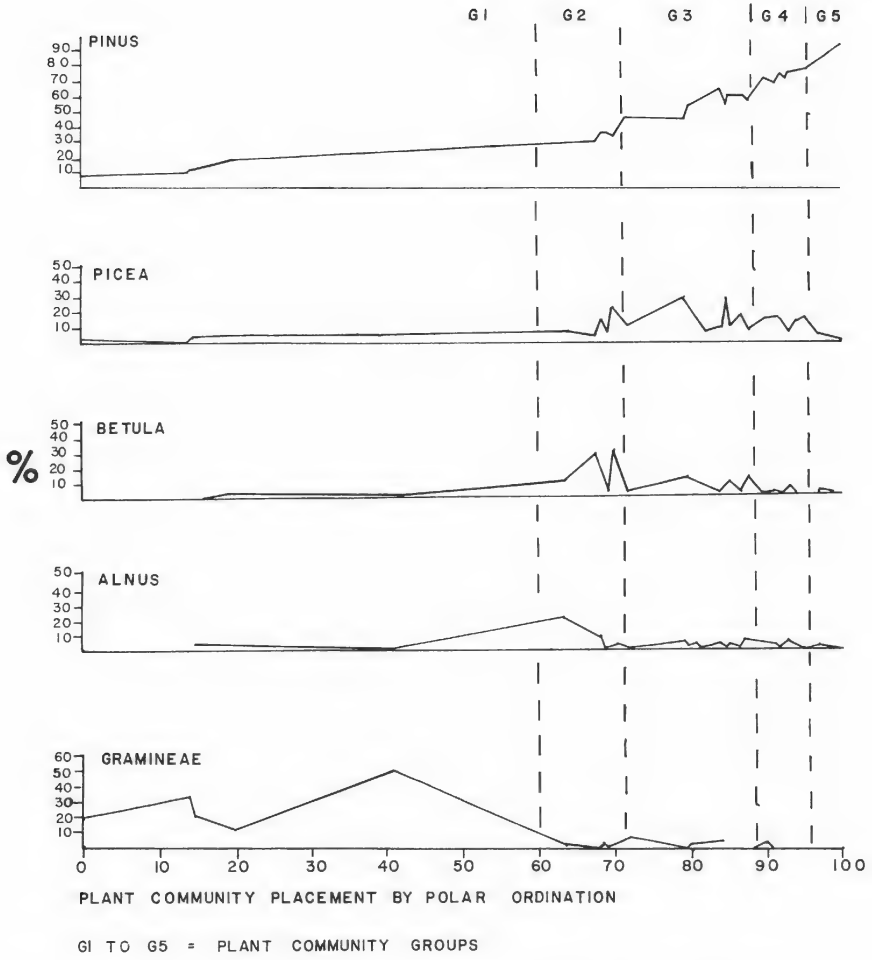

Figure 2. Relationship of selected pollen taxa to community placement by Polar Ordination.

tional and the pollen data, I used a correlation analysis available through the SAS package (Hedwig and Council 1979). The results are presented in Table 3.

The correspondence between the surface pollen spectra and the vegetational composition is close. Using the groups of stands delimited by the ordination of the palynological data, the types of vegetational stands included within each group can be examined.

Group 1. These five stands (no. 1-5) were all located in the southeastern portion of the province, and vegetationally were all described as grassland communities. Gramineae, as expected, dominated the vegetational record. *Artemisia* sp. was also present in large quantities. *Pinus* pollen was present in the surface samples in frequencies ranging from 7-24 percent, although it was absent in the vegetation. Gramineae pollen was high (13-50 percent) as was that of *Artemisia* (1-45 percent). Cheno-am (pollen

TABLE 3. Correlation coefficients of vegetational and pollen data.

	Pearson Correlation Coefficient	
	Pollen	Plant
Pollen	1.00000	0.66938
Plant	0.66938	1.00000
	Spearman Correlation Coefficient	
	Pollen	Plant
Pollen	1.00000	0.53135
Plant	0.53135	1.00000
	Kendall Tau B Correlation Coefficient	
	Pollen	Plant
Pollen	1.00000	0.37238
Plant	0.37238	1.00000
	Pollen	Plant

of the family Chenopodiaceae and the genus *Amaranthus*) pollen was also present (2-12 percent), but again, no specimens of this taxon were observed in the stand.

Group 2. The five stands in this group (no. 6-10) varied in their vegetational composition. Pine pollen ranges from 30-37 percent, *Picea* from 5-25 percent, and *Betula from* 7-31 percent. While the vegetational composition was varied, some correlations were present. Four of the five communities did not have a well developed canopy. Most of the stands in this group were located in the transitional area between the parkland and the boreal forest (no. 7, 9), or were located in the southern boreal forest region identified by Rowe (1972) as the Mixedwood forest region (no. 8, 10). Stand no. 6 was an alpine tundra located near Mt. Edith Cavel in the Jasper National Park. This stand probably clustered with this group because of the reduced pine frequencies.

Group 3. Ten stands (no. 11-20) were included within this group. These stands were principally dominated by aspen (*Populus tremuloides*) and varying percentages of birch (*Betula papyrifera*). Stand no. 11, 12, 16, 18, and 20 (all small and isolated) were not dominated by *Populus* but were located within the area described as the aspen parkland. Pine pollen was intermediate in frequency (45-66 percent), and *Picea* pollen increased to its highest mean frequency (16 percent). *Populus* pollen ranged from 0-4 percent, but this is not unusual because this taxon is normally underrepresented in pollen assemblages (Sangster and Dale 1961, 1964; Holloway 1981) due to poor preservation. *Betula* and *Alnus* pollen are present in moderate amounts (3-14 percent and 2-12 percent, respectively). Rosaceae and Fricaceae pollen are relatively high (4 percent), given their dispersion mechanism and low pollen production, and both indicate the well developed understory component of these stands.

Group 4. This group consisted of stand no. 21-27, and most were dominated by black spruce (*Picea mariana*), larch (*Larix laricina*), or pine (*Pinus contorta*). In addition, most sites contained an understory dominated by *Ledum* and other herbaceous taxa. This understory was not as well developed as those in Group 3 stands. Pine pollen percentages were quite high, ranging from 70-78 percent. *Picea* pollen is also high (5-18 percent) with *Betula* and *Alnus* present but in lower frequencies. One stand (no. 26) was dominated solely by *Populus tremuloides.*

Group 5. This group consisted of the final two stands (no. 28, 29), both dominated by *Pinus contorta.* The surface pollen assemblage reflects this vegetational dominance as *Pinus* pollen is present in excess of 85 percent.

Discussion

The degree of correspondence between the surface pollen rain and the vegetational composition is significant, as shown by the correlation coefficient of 0.66 (Table 3). However, other factors may also be responsible for the observed distribution of the pollen.

Pinus produces larger quantities of pollen that are easily dispersed by the wind. Over one million grains of pollen are produced by each male strobilus (Erdtman 1969); thus, it is not surprising that pine pollen was recovered from several communities in which the taxon was not physically present.

Many of the understory plants of these communities are insect pollinated and therefore produce only small numbers of pollen grains per anther. The presence of any of these entomophilous pollen types in the pollen spectra, even in very low frequencies, usually indicates a well developed herbaceous component. Other pollen grains, such as *Larix* and *Populus,* are thin-walled and do not preserve easily even under ideal conditions (Sangster and Dale 1961, 1964; Holloway 1981). Thus, the pollen spectra would not be expected to reflect accurately the precise vegetation composition of the dominant tree species in a community composed of taxa whose pollen preserved poorly (Mack and Bryant 1974, Mack *et al.* 1978).

The results of the ordination have revealed that the percentages of pine pollen is an important factor in the ordering of the stands. Pine pollen is easily dispersed and is usually over-represented, especially in communities in which pine was not present. Thus, the proximity and density of pine stands to other vegetational communities is largely responsible for the distribution of pine pollen in the local and regional pollen rain. Pines are primarily dominant in the foothills region of Alberta (Rowe 1972), located east of the front range along the western boundary of the province. Since winds are primarily westerlies, *Pinus* pollen is easily dispersed to adjacent, more easterly plant communities.

Muskeg communities (Group 4) are more typically present in the western portion of the province, or scattered within blocked drainage depressions irregularly distributed throughout the southern areas of the Boreal Forest (Rowe 1972). These are wetter sites where spruce dominates the canopy. Local stands of pine may be found on drier, well-drained uplands, but only rarely are other arboreal elements in close proximity to these stands. The large pollen production of nearby pine stands often masks the lower production of *Picea* pollen distribution in these muskegs. As indicated in Table 1, however, this community-type can still be recognized by slight increases in the percentage of spruce pollen. Even though the muskeg community-type is often discontinuous, small pine stands are sometimes in close proximity to them. The presence of these pine stands often effectively obscures the local production of spruce pollen, and this over-representation of pine pollen virtually eliminates the presence of other pollen taxa from inclusion within the pollen record.

Aspen stands (*Populus tremuloides*) are common in both the Aspen Grove and Mixedwood forest regions (Rowe 1972). According to the data recovered from the surface pollen spectra, communities located within each of these forest areas can be identified even though the presence of *Populus* pollen is small. The Aspen Grove region is primarily an ecotone between the forest and the grasslands (Moss 1932, Rowe 1972). Dominant species include *Populus tremuloides*, with sub-dominants of

balsam poplar (*P. balsamea*), *Betula* sp., and *Alnus* sp. In the western portion of this area, representatives of this sub-alpine forest are present, commonly forming a spruce-aspen ecotone. Since *Populus* pollen preserves poorly, larger percentages of *Picea* pollen are often present. Pine is also farther removed from these stands and contributes less pollen to the surface assemblage, and therefore the local pollen production is masked more by *Picea* pollen than by the pine pollen. The presence of other arboreal species in the Aspen Grove is indicated by smaller percentags of *Betula* and *Alnus* pollen. Finally, since these stands are generally open with a well developed herbaceous level, minor increases in Gramineae pollen are recorded in stands from this region.

The Mixedwood (Rowe 1972) is composed of a variety of arboreal species. The dominance of *Betula* and *Alnus* pollen in these Mixedwood assemblages is interpreted as a result of their high pollen productivity and their more successful preservation. While pine and spruce are present within this forest region, their distribution is somewhat restricted. The restrictive occurrence of both *Pinus* and *Picea* in this community-type act to increase the relative pollen frequencies of *Betula* and *Alnus* pollen, which in turn is responsible for clustering of these stands.

The grassland communities are far enough removed from the pine sources so as to contribute little to the surface pollen rain. These stands are clearly dominated, palynologically, by taxa that are present in the vegetational composition, Gramineae and *Artemisia*. This increase in Gramineae, Cheno-Am, and *Artemisia* pollen effectively characterizes these grassland communities.

As stated earlier, the one stand recovered from an alpine tundra was an anomaly. This stand clustered with the Mixedwood stands (Group 2). Its high altitude location effectively removed it from distant *Pinus* pollen sources. The vegetation of this stand was dominated either by relatively low pollen producing plants (such as Rosaceae and shrub forms of *Picea* and *Salix*) or by plants whose pollen production had been curtailed by local conditions.

Conclusions

Polar ordination is an effective and simple method for differentiating regional plant community associations based on their surface pollen rain. By reducing the recovered vegetational data base to its lowest common denominator, a more nearly precise analysis of the relationships can be obtained. Using modern surface pollen frequencies, the stands were clustered by ordination into groups that corresponded not to the vegetational composition of the stand but rather to the vegetational component of the major plant associations located within the province.

The inferred gradient obtained by ordination appears to mirror the latitudinal distribution of these plant associations. These associations follow the decreasing pine pollen percentages from areas with high pine pollen (the western montane forests) to those where pine pollen is low (grasslands).

Since polar ordination has been effective in delimiting plant associations based on surface pollen assemblages, it should likewise be useful in grouping fossil pollen assemblages that contain similar component taxa. While small, local vegetational differences will normally not be identified, the results of this study show that major plant associational differences, as reflected by the regional pollen rain, can be identified. The differentiation of major plant associations as revealed through use of pollen or-

dination may, perhaps, also be a beneficial technique for use with fossil pollen records. If fossil pollen samples within a continuum (such as those recovered from lake or bog cores) are treated as discrete community samples, much like the surface pollen spectra discussed in this study, then those levels with similar pollen rain will probably cluster together. The application of polar ordination techniques to the fossil pollen record may reveal additional, quantifiable data concerning changes in major plant associations and successional patterns than are apparent only by use of other standard techniques.

To test this hypothesis, fossil pollen data already available from Central Alberta (Holloway *et al.* 1981) will be analyzed using this technique. The results of this ongoing research should elaborate the successional and migration patterns of major plant associations throughout this region of central Alberta during the past 16,000 years and should demonstrate the utility of the polar ordination technique in fossil pollen studies.

Acknowledgments

I thank Drs. Vaughn M. Bryant, Jr., David L. Carlson, and D. Bruce Dickson for their valuable critiques on earlier versions of this manuscript. I am especially grateful to Dr. Fred Smeins for his advice and for supplying the computer program. Thanks are also extended to the Anthropological Research Laboratories at Texas A&M University for use of their facilities and computer time.

Literature Cited

Adams, D. P., and P. J. Mehringer. 1975. Modern pollen surface samples: an analysis of subsamples. J. Res. U.S.G.S. 3:733-736.

Barkley, F. A. 1934. The statistical theory of pollen analysis. Ecology 47:439-447.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 37:325-349.

Brooks, D., and K. W. Thomas. 1967. The distribution of pollen grains on microscope slides. Part I. The non-randomness of the distribution. Pollen et Spores 9:621-629.

Cross, A. T., S. N. Stephanson, and M. A. Bordner. 1980. Some comparisons of pollen and spore distribution in surface sediments to modern vegetation in Baja California, Mexico. Abstracts of eleventh annual meeting A.A.S.P. Palynology 4:238.

Daubenmire, R. 1974. Plant Communities: a Textbook of Synecology. Harper & Row, New York.

Erdtman, B. 1960. The acetolysis method: a revised description. Svsk. Botan. Tdsk. Bd. 54 II.4.

———. 1969. Handbook of palynology. Hafner Pub. Co., New York.

Faegri, K., and J. Iversen. 1975. Textbook of Pollen Analysis. Munksgaard Press, New York.

Fine, B. 1980. Two quantitative methods applied to modern pollen data from tropical Mexico. Abstracts of the eleventh annual meeting A.A.S.P. Palynology 4:240.

Gauch, H. G. 1977. Ordiflex Release B. Cornell University, New York.

Goodall, D. W. 1953. Factor analysis in plant sociology. Paper read to third Internat. Biometric Conf. in Bellagio.

Hansen, H. P. 1946. Post-glacial forest succession and climatic change in Oregon Cascades. Amer. J. Sci. 244: 710.

———. 1949a. Postglacial forests in south central Alberta, Canada. Amer. J. Bot. 36:54-65.

———. 1949b. Postglacial forests in west central Alberta, Canada. Bull. Torrey Bot. Club 76:278-289.

Hedwig, J. T., and K. A. Council. 1979. SAS User's Guide. Raleigh, N.C.

Heusser, C. J. 1977 Modern pollen spectra from western Oregon. Bull. Torrey Bot. Club 105-14-17.

Holloway, R. G. 1981. Preservation and experimental diagenesis of the pollen exine. Ph.D. thesis, Texas A&M Univ., College Station, Texas.

———, V. M. Bryant, Jr., and S. Valestro. 1981. A 16,000 year pollen record from Lake Wabamun, Alberta, Canada. Palynology 5:195-208.

Jackson, L. E. 1979. New evidence for the existence of an ice free corridor in the Rocky Mountain foothills near Calgary, Alberta during late Wisconsin Time. Current Res. Part A. Geol. Sur. Can. Paper 79-1A:107-111.

Janssen, C. R. 1970. Problems in the recognition of plant communities in pollen diagrams. Vegetatio 20:187-195.
King, J. E., and R. O. Kapp. 1963. Modern pollen rain studies in eastern Ontario. Can. J. Bot. 41:243-252.
Kroker, S. J. 1979. Late Holocene paleocology of the Hand Hills region of Alberta: implications for archaeological research. M.A. thesis, Univ. of Manitoba, Winnipeg.
Lichti-Federovich, S. 1970. The pollen stratigraphy of a dated section of late-Pleistocene lake sediment from central Alberta. Can. J. Earth Science 7:938-945.
———. 1972. Pollen stratigraphy of a sediment core from Alpen Siding Lake, Alberta. Geol. Sur. Can. Paper 72-1 (Part B):113-115.
Mack, R. N., and V. M. Bryant, Jr. 1974. Modern pollen spectra from the Columbia Basin, Washington. Northw. Sci. 48:183-193.
———, ———, and W. Pell. 1978. Modern forest pollen spectra from eastern Washington and northern Idaho. Bot. Gaz. 139:249-255.
Margraf, V., H. L. D'Antoni, and T. A. Ager. 1981. Modern pollen dispersal in Argentina. Palynology 5:43-63.
McAndrews, J. H., and H. E. Wright. 1969. Modern pollen rain across the Wyoming basin and the northern great plains (U.S.A.). Rev. Paleobot. Paly. 9:17-43.
Moss, E. H. 1932. The vegetation of Alberta IV: the poplar association and related vegetation of central Alberta. J. Ecol. 20:380-415.
———. 1974. Flora of Alberta. University of Toronto Press, Toronto.
Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons Inc., New York.
North, M. E. A. 1976. A Plant Geography of Alberta. Dept. Geogr. Monogr. No. 2 Univ. of Alberta, Edmonton.
Rowe, J. S. 1972. Forest Regions of Canada. Dept. Envir. Can. For. Ser. Pub. No. 1300.
Rowley, J. R. 1955. A study of the recent pollen at Lake Itasca biological station. Proceed. Minn. Acad. Sci. 23:50-60.
Sangster, A. G., and H. M. Dale. 1961. A preliminary study of differential pollen grain preservation. Can. J. Bot. 39:35-44.
———. 1964. Pollen grain preservation of underrepresented species in fossil spectra. Can. J. Bot. 42:437-499.
Webb, T. III, and J. H. McAndrews. 1976. Corresponding patterns of contemporary pollen and vegetation in central North America. Geol. Soc. Am. Memoir 145:267-299.
Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 42:207-264.

Received June 28, 1982
Accepted for publication December 2, 1982

Robert Steele

USDA Forest Service
Intermountain Forest and Range
Experiment Station
Forestry Sciences Laboratory
316 E. Myrtle St.
Boise, Idaho 83702

An Approach to Classifying Seral Vegetation within Habitat Types

Abstract

A concept for classifying seral vegetation within habitat types is presented. Conceptual illustrations and field data examples from the *Abies grandis/Vaccinium globulare* habitat type are used to demonstrate the classification. Prognostic capability of this technique is discussed.

Introduction

The dynamics of plant communities present a complex and often bewildering set of interacting variables. Conceptually, these variables can be grouped under two primary forces affecting vegetation: time and environment. Vegetation reflects time through successional development, which can be erased, altered, or accelerated by various disturbances. Vegetation reflects environment through climax communities (Daubenmire 1952), which are relatively stable barring disturbance or alteration of the environment. The complex environments of Northern Rocky Mountain forests have been recently subdivided by habitat type classification systems (Daubenmire and Daubenmire 1968, Pfister *et al.* 1977, Steele *et al.* 1981), which focus on potential climax vegetation. The habitat type approach has been tested in many areas of the West and proven useful to natural resource managers (Layser 1974), yet no classification with similar capabilities exists for successional (temporal) aspects of vegetation. This paper presents a classification system designed to meet that need and to interface with the habitat-type system.

Concepts

Although there is considerable information on plant succession, simulation modeling, and plot grouping techniques (Shimwell 1971, Mueller-Dombois and Ellenberg 1974, West *et al.* 1981) there are few concepts that deal systematically with classifying the temporal aspects of seral vegetation. Many vegetation classifications used today either are largely descriptive, emphasizing plant cover (Kuchler 1966, Eyre 1980), or focus on identifying site differences (Daubenmire 1952) Krajina 1965). The former group offers little ecologic prediction capability for land management and often treats only the dominant vegetal layer; the latter group, which has been expanded recently over the western U.S. (Pfister 1977), provides high prediction capability between classified environments but does not classify seral stages within environments. Classifications of the Braun-Blanquet (1932) approach are somewhat intermediate in utility and focus on species composition and structure that do not always subdivide environment. One

land resource planning model (Henderson and West 1977) provides for temporal classification within habitat types but lacks the field data needed to develop site-specific output. Arno and Simmerman (1982) studied successional sequences in four habitat types and subdivided the time gradient by using classic structural stages such as shrub, sapling, pole, and mature forest. Their diagrammatic classification somewhat resembles the conceptual system presented here.

The lack of concepts addressing succession classification may stem from past philosophies coupled with a past lack of suitable environmental classification. Gleason (1927) stated that succession "is no more than the mass effect of the action or behavior of individual plants," and hence any stage of succession need not "follow an orderly sequence in its development." This assumption would seem to preclude a systematic classification of seral communities. However, the general environment of each sere can be classified by using the habitat-type approach, most easily done when some near-climax vegetation remains in the area. Each classified macroenvironment (habitat type) in turn determines which species can potentially occupy the site during various successions. This environment also determines which species have potential to become well represented, as opposed to gaining only a minor foothold on the site. ("Well represented," herein, is any canopy coverage >5 percent of the land area in question.) The potentially well-represented species within one habitat type can be arranged according to their succession-sequence characteristics, such as early seral vs. climax. This arrangement then provides the basis for developing successional classification within a given habitat type.

Focusing on potential seral species and their relative succession-sequence characteristics avoids the need for first predicting actual successional pathways, which, as Gleason (1927) suggests, may be random. If successional pathways become predictable, the predictions and classification structure should corroborate each other. Thus, a successional classification design to accommodate individual species behavior will handle equally well those successional studies that may follow less individualistic approaches. However, the converse may not be true.

Certain analogies with the habitat type classification help convey conceptual aspects of the following successional classification:

1. Habitat type classifications are based on climax plant communities, thus holding time relatively constant while the environmental gradient is being subdivided. Similarly, successional classification should hold environment relatively constant by means such as habitat types while the time gradient is being subdivided.
2. Habitat-type classification characterizes environment from the integrated expression of the potential climax plant community rather than from weather and soils data. Likewise, succession classification should characterize successional time from relative stages of community development rather than from number of years or growing seasons. Years do not measure successional advance because some years or growing seasons may only maintain the existing community. As suggested by many persistent seral communities, successional advance depends on less predictable occurrences such as seed production, seed predators or diseases, annual weather patterns, existing species composition, and combinations thereof. Although investigators often relate seral communities to years since disturbance, a severe disturbance can convert a near-climax community to an early seral stage, while a similar site disturbed less severely at the same time can result in a mid-

seral stage. Consequently, notations that characterize relative stage of development would more consistently place plant communities in their appropriate successional positions.

3. Classification of environment by habitat type employs indicator species according to their relative ecologic amplitudes (relative vulnerability to environmental change) and ability to dominate at climax (Steele *et al.* 1981). Similarly, classification of successional time by relative stage of development should employ indicator species according to their relative vulnerability to successional change and ability to dominate certain successional stages. In developing this concept, plant community coverage data from 375 m^2 plots (Pfister and Arno 1980) were taken in various seral stages within one habitat type. Some data for near climax stages were taken from a previous study (Steele *et al.* 1981). Known successional roles of the sampled species were subjectively compared with various attributes such as life form, reproductive strategies, natural longevity, relative tolerance to shade, possible allelopathic interactions, and resistance to disease and insects. Some of these attributes have predictive value in succession simulation models (Noble and Slatyer 1977, Cattelino *et al.* 1979). The results showed that relative vulnerability to successional replacement is the most useful indicator for subdividing the succession sequence. This characteristic reflects the integrated effects of the combined above attributes of individual species during succession and is interpreted through relative decline in canopy cover. Species dominance is also needed to characterize community structure. Neither characteristic alone nor any of the individual attributes consistently places a community in its logical successional position.

The Model

The secondary succession model by Huschle and Hironaka (1980) provides an initial framework for developing the successional classification concepts. Their cone-shaped model projects a convergence of many seral community types toward one climax community and suggests a structural framework for systematically classifying seral vegetation. Their model was developed for nonforest communities but applies equally well to forest communities and even to the tree, shrub, and herbaceous layers separately. The framework of their model suggests delineation of vegetation according to relative successional stage and emphasizes the potential complexity of seral vegetation within one habitat type.

Forest communities often have several vegetation layers at different successional stages, each likely proceeding at a different rate. Therefore, this classification first stratifies a plant community by layers—tree, shrub, herbaceous. In each layer, the well-represented species most vulnerable to successional decline is combined with the dominant species of that layer to delineate a temporal-structural unit of vegetation. Since the habitat type determines which species are potentially well represented and any well-represented species may be a potential dominant, temporal-structural units for all possible seres within a habitat type can be established once the major seral species and their relative vulnerabilities are known. These units, called layer types, can be arranged to form a classification model. In this model (Fig. 1), the bottom row of layer types represents possible combinations of the earliest seral indicator (most vulnerable species) with the potential dominants of that particular vegetation layer; relative vulnerability

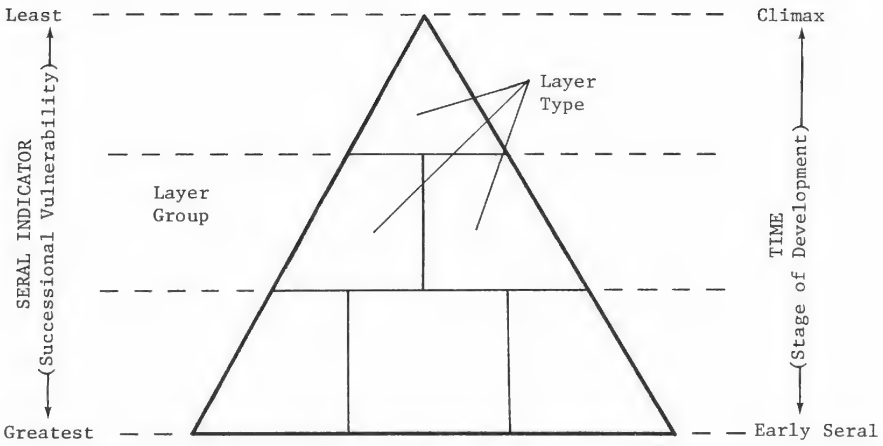

Figure 1. Basic structure of succession classification model.

of seral indicators progressively decreases upward toward climax. Since increasingly fewer species have potential to dominate toward climax, increasingly fewer units are possible and the triangular model results. In three dimensions, Figure 1 resembles the basic cone-shaped model of Huschle and Hironaka (1980). To maintain a systematic nomenclature, each taxonomic unit is called a layer type, and each group of layer types having the same seral indicator is called a layer group.

Examples

The Tree Layer

With forest habitat types, the clearest examples of this classification approach occur in the tree layer. In the *Abies grandis/Vaccinium globulare* (*ABGR/VAGL*) habitat type (Steele *et al.* 1981), *Abies grandis*, *Pseudotsuga menziesii*, and *Pinus contorta* are the major tree species. *Larix occidentalis, Picea engelmanii,* and *Pinus ponderosa* are also occasionally present, but are omitted to simplify this explanation. Consider these three major species on the same site, each one well represented. From general knowledge that *Pinus contorta* can be succeeded by *Pseudotsuga*, which in turn can be succeeded by *Abies grandis,* one can visualize *Pinus contorta* as an indicator of the earliest successional stage, *Pseudotsuga* the secondary successeional stage, and *Abies* as the climax dominant. Although unforeseen factors may preclude the entire replacement sequence, the relative vulnerability to replacement has been established. These three indicator species are then combined with the possible dominants to form the classification model found in Figure 2. The first species of each unit in this model is the seral indicator (most vulnerable); the second species is the dominant (greatest canopy coverage). As Figure 2 shows, a *Pico-Abgr* layer type would have *Pinus contorta* (and possibly *Pseudotsuga*) well represented in the stand, but *Abies grandis* would have the greatest canopy coverage regardless of relative heights. This nomenclature provides a simple general description of relative successional position and present structure for the tree layer. The same framework applies to the other vegetation layers. Names for each vegetation layer are then combined to characterize the entire plant community.

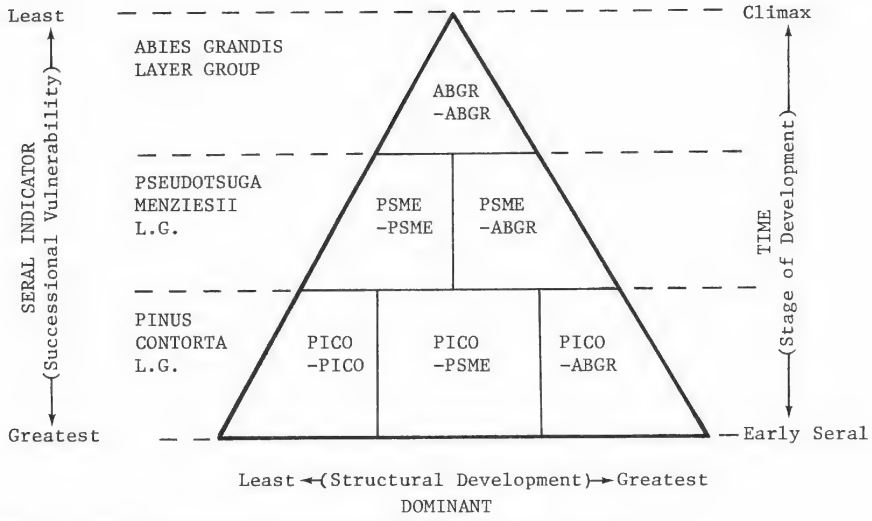

Figure 2. Example of succession classification model using the tree layer.

A key to layer types (Table 1) is easily derived from the classification model (Fig. 2). Seral indicators are delineated at the point where their canopy coverage ceases to be well represented (>5 percent coverage). The key should start with the most vulnerable indicator species and progress along the time gradient to climax (Table 1). Where appropriate, seral indicators with similar relative vulnerabilities can be combined to simplify the classification. Such groupings are most apt to occur in the shrub and herb layer classifications for which similar keys can be written. The arbitrary use of 5 percent canopy coverage may also be adjusted to better accommodate actual situations. Usually, relative shade tolerance is the main species attribute acting in the tree layer, but other attributes previously mentioned may also be involved. The integrated effects of these individual attributes during succession is reflected in the relative vulnerability of each species as outlined in the key.

This exercise illustrates the actual approach used for the shrub and forb layers. But because the tree layer goes through recognizable size classes of development such as sap-

TABLE 1. Example of key to tree layer groups and layer types as derived from Figure 2.

1.	All tree species (>4.5 ft tall) poorly represented[1]	depauperate tree layer
1.	At least one species (>4.5 ft tall) well represented[1]	2
2.	Pinus contorta well represented	PICO Layer Group
	2a. Pinus contorta dominant	Pico-Pico Layer Type
	2b. Pseudotsuga menziesii dominant	Pico-Psme Layer Type
	2c. Abies grandis dominant	Pico-Abgr Layer Type
2.	P. contorta poorly represented	3
3.	Pseudotsuga menziesii well represented	PSME Layer Group
	3a. Pseudotsuga menziesii dominant	Psme-Psme Layer Type
	3b. Abies grandis dominant	Psme-Abgr Layer Type
3.	P. menziesii poorly represented	4
4.	Abies grandis well represented	ABGR Layer Group
	4a. Abies grandis dominant	Abgr-Abgr Layer Type

[1]Well represented is arbitrarily defined as having a canopy coverage greater than 5% of the land area; poorly represented is less than 5%.

ling (.24-10.2 cm; .1-4 in, d.b.h.[1]), pole (10.2-30.5 cm; 4-12 in), mature (30.5-45.7 cm; 12-18 in) and old growth (>45.7 cm; >18 in), these additional subdivisions should be noted. These notations are best added to each tree species after the tree layer type (l.t.) is identified, such as Mature *Pico*-Sapling *Abgr* l.t. For consistency within the classification, the smallest size class present that applies to the key (Table 1) should be selected as the notation. This procedure is followed because the larger size classes usually decline first during succession, and the layer group indicator species is not actually replaced until it is represented by less than 5 percent canopy cover, regardless of size class. Also, the youngest size class best depicts the appropriate seral stage because it represents the reproductive status of the most vulnerable tree species in the sere. Figure 3 illustrates the subdivisions within layer types that can result from combinations of seral indicators and dominant when size class notations are used.

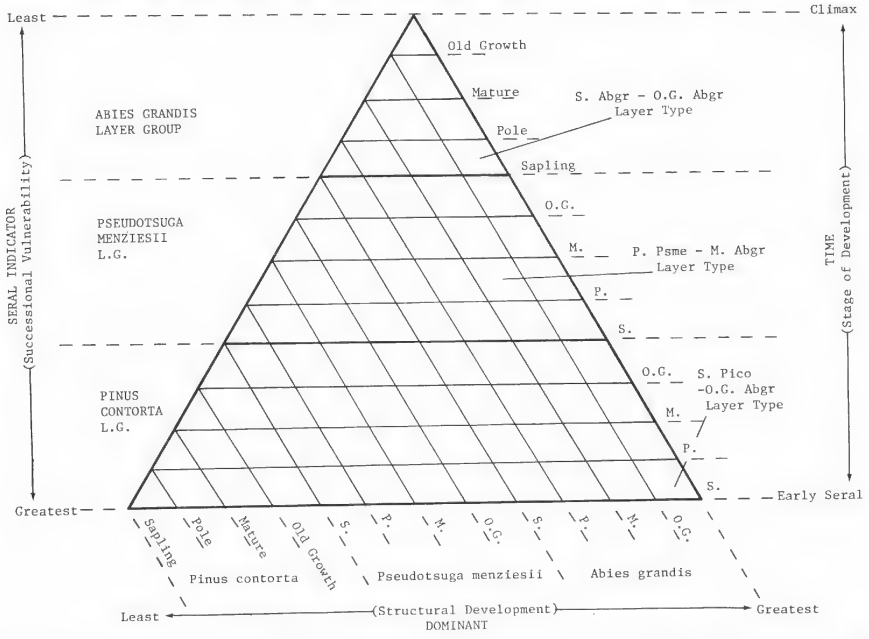

Figure 3. Tree layer subdivisions (using size class notations) as indicated by combinations of successional indicator and dominant.

At first, visualizing some tree layer types in their appropriate successional position may be difficult. For instance, a Sapling *Abgr.* l.t. woult not seem to be more successionally advanced than an Old Growth *Pico*-Pole *Abgr* l.t., because we think of these seres in terms of years of development. But in terms of their relative position along the successional gradient, a pure stand of Sapling *Abgr* is closer to potential climax than a mixed older stand of *Pico* and *Abgr* because, lacking disturbance, it will not go through the earlier successional stages of the *PICO* and *PSME* layer groups. In fact, a Sapling *Abgr* l.t. may even reach climax in fewer years than an Old Growth *Pico*-Sapling *Abgr*

[1]d.b.h. diameter at breast height (4½ ft.).

l.t. if the latter has *Pseudotsuga* well represented and must pass through a long lived *Psme-Abgr* l.t.

The Shrub Layer

Shrub layers in the *ABGR/VAGL* habitat type contain more seral species than the tree layer and thus generate more possible units within the classification model. For example, various seral stages were sampled in 58 plots scattered throughout the range of *ABGR/VAGL* in central Idaho; 54 of these plots had at least one shrub species well represented. Six shrub species were well represented among the 54 plots. The possible combinations of seral indicator and dominant using these six species result in 21 layer types (Fig. 4).

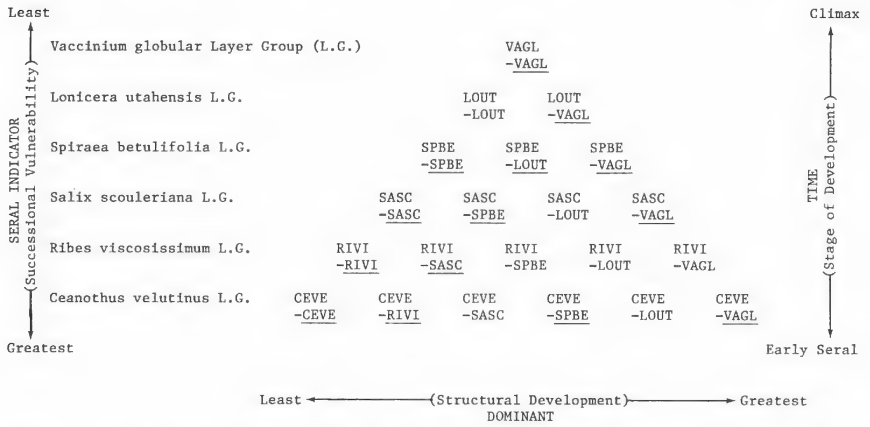

Figure 4. Classification model of possible shrub layer types in *Abgr/Vagl* habitat type; underlined layer types are represented by field data.

The formula for the triangular matrix of N layer types is $N = \frac{n^2 + n}{2}$, where $n =$ the number of species involved; in this case, $n = 6$. Of these 21 types, 14 appear in the data set. The remaining seven may either appear following disturbance patterns and intensities that differ from those of the past or may be rare, regardless of site history.

When sufficient data are available, analysis of synthesis tables (Mueller-Dombois and Ellenberg 1974) provides insight to the relative vulnerabilities of the species involved and a basis for adjusting the classification model. Individual plot data and groupings by layer type can be subjectively arranged from early seral to climax on the horizontal axis. A similar arrangement on the vertical axis should list the well-represented species according to relative vulnerability. Arrangements along both axes can be adjusted so that points where species cease to be well represented reflect a logical progression of decreasing vulnerability that coincides with a logical progression of the stands toward climax. The species that first ceases to be well represented is considered the most vulnerable and is placed at the bottom of the classification model (Fig. 4). Other species are placed in their appropriate relative positions. Table 2 lists pertinent data extracted from the final analysis of a synthesis table. These data reflect a logical relative decline in average coverage of seral species that parallels the general successional sequence of stands sampled in the *ABGR/VAGL* habitat type. Shrub layer groups show groupings

TABLE 2. Constancy[1] and average coverage percent[2] (the latter in parentheses) of major seral shrubs[3] in ABGR/VAGL habitat type.

LAYER GROUP	Ceanothus velutinus						Ribes viscosissimum					Salix scouleriana				Spiraea betulifolia			Lonicera utahensis		Vaccinium globulare
SHRUB LAYER TYPE	Ceve -Ceve	Ceve -Rivi	Ceve -Sasc	Ceve -Spbe	Ceve -Lout	Ceve -Vagl	Rivi -Rivi	Rivi -Sasc	Rivi -Spbe	Rivi -Lout	Rivi -Vagl	Sasc -Sasc	Sasc -Spbe	Sasc -Lout	Sasc -Vagl	Spbe -Spbe	Spbe -Lout	Spbe -Vagl	Lout -Lout	Lout -Vagl	Vagl -Vagl
Number of Stands	n=4	n=1	.	n=1	.	n=2	n=3	n=1	.	.	.	n=1	n=3	.	n=7	n=3	n=1	n=4	.	n=13	n=10
SHRUB SPECIES																					
Vaccinium globulare	8(2)	10(2)	.	10(2)	.	10(26)	7(T)	10(15)	.	.	.	10(1)	10(22)	.	10(68)	7(T)	10(2)	10(62)	.	10(69)	10(52)
Lonicera utahensis	5(9)	10(2)	.	—	.	10(8)	10(10)	10(2)	.	.	.	10(T)	7(T)	.	10(15)	7(T)	10(15)	10(14)	.	10(15)	10(2)
Spiraea betulifolia	10(5)	10(2)	.	10(20)	.	10(8)	3(T)	—	.	.	.	10(2)	10(31)	.	9(6)	10(22)	10(15)	10(15)	.	8(2)	7(2)
Salix scouleriana	5(20)	10(2)	.	10(T)	.	10(1)	10(2)	10(15)	.	.	.	10(62)	10(20)	.	10(16)	7(2)	10(T)	5(1)	.	4(2)	6(1)
Ribes viscosissimum	5(8)	10(15)	.	—	.	10(1)	10(18)	10(15)	.	.	.	—	7(T)	.	7(T)	10(1)	10(T)	2(T)	.	5(1)	6(1)
Ceanothus velutinus	10(38)	10(15)	.	10(15)	.	10(15)	7(T)	10(2)	.	.	.	10(2)	7(2)	.	—	2(T)	10(T)	—	.	—	1(2)

[1]Code to constancy values. + = 0-5% 1 = 5-15% 2 =15-25% 3 = 25-35% 4 = 35-45% 5 = 45-55% 6 = 55-65% 7 = 65-75% 8 = 75-85% 9 = 85-95% 10 = 95-100%

[2]T = Trace,

[3]Underlined values show where a species serves as a seral indicator.

of stands beyond which a particular seral indicator ceases to be well represented. For instance, *Ceanothus velutinus* (most vulnerable) is well represented only in the earliest seral stages of the shrub layer, whereas *Vaccinium globulare* (least vulnerable) can be well represented throughout the data from early seral to climax. Occasionally, two species will display similar vulnerabilities and can be grouped when constructing the key to layer types.

Discussion

Although the Huschle and Hironaka (1980) succession model and the classification model (Fig. 1) have similar patterns, the classification model should not be construed as predicting successional pathways, even though it illustrates the many possibilities. As shown in Figure 1, succession on a given site only progresses upward in the form of species replacement between layer groups. Progression to the right within a layer group is treated as structural development to distinguish it from the upward advance between layer groups. In reality, a shift in either direction is a form of succession. Retrogressive changes from disturbance cause a shift downward or to the left. Changes in any direction seldom occur in stepwise progression and generally skip many layer types and even layer groups. Predicting change requires comparison of existing and potential composition of individual stands with the relative position of that stand in the classification model. Predictions of retrogressive changes must also consider the type and intensity of disturbance. Even though some layer types are relatively common and others quite rare, generalized pathway predictions must be made from field observations.

The classification models (Figs. 2, 4) may seem too complex for practical use. A simplistic classification is always the most desirable, but oversimplification can reduce accuracy. An adequate classification of any system must have enough taxonomic units to accomodate its components. The classification herein delineates vegetation according to the possible successional units occurring through time. Because not all units may exist on the landscape at one time, this classification may appear more complex than necessary. But if all possible vegetation within one habitat type could be surveyed, the classification design would appear adequate rather than overly complex.

This classification provides ecologic prediction capability and implications for land management. For example, each shrub layer potentially occurring in the *ABGR/VAGL* habitat type can be located within the model (Fig. 4). The relative position of a given shrub layer in the model indicates whether succession or disturbance is needed to convert that shrub layer to some other shrub layer. The model also suggests the intensity of disturbance (in terms of species to be removed) that may be needed to achieve the desired layer type. For instance, if a *Spbe-Vagl* l.t. is disturbed lightly enough to remove *Vagl* but not enough to introduce *Ceanothus*, *Ribes*, or *Salix*, it will only shift to the left in the *SPBE* layer group. But if it were severely burned, it may shift downward to the *SASC* or *CEVE* layer group or, if severely scarified, the *RIVI* layer group or possibly no shrub layer at all. However, composition of each stand must be examined to determine if that particular community has potential to produce the desired layer type from a given treament. Considerable study is needed on reaction of many species to types and intensities of disturbance.

Large disturbed areas often contain more than one habitat type. As the Huschle and Hironaka (1980) model suggests, one seral community may overlap different habitat

types, especially in early seral stages. Vegetative potential, total species composition, and management implications may vary even though classification models for different habitat types result in the same name for the overlapping community. Trained personnel can extrapolate habitat types from adjacent, less disturbed areas by considering terrain features and often subtle differences in species composition. In some cases, comparison of succession classification models with existing seral vegetation may also indicate which habitat type exists. When habitat types cannot be delineated, the more severe of the two habitat types in question should be used for management purposes. Management plans can be revised as successional advance makes the habitat types more discernible.

With this classification approach, seral vegetation can be tentatively classified without the entire classification structure being formalized. The field investigator need only determine which well-represented species in a given layer has the greatest vulnerability to successional replacement and which species is dominant. After these determinations and supporting coverage values are collected for a number of stands, they can be synthesized (Table 2) and applied to classification models (Figs. 2, 4) to develop layer types. Accuracy of the field worker can be improved by first developing a tentative list of species according to their suspected relative vulnerability to succession. Partial listings may be derived from sample data previously collected for habitat-type classification studies.

The main use of this classification is to relate one plant community to all others in the same habitat type in terms of relative successional stage. Understanding such relationships provides ecologic prediction capability and a communication base. Even though the models outline possible successional directions and possible layer types within a habitat type, they do not diagram successional pathways. Actual pathways must be developed from examination of species composition within individual stands and known successional trends. Stages of a particular pathway, however, can be expressed in terms of the layer types presented and linked as outlined in the classification models.

Acknowlegments

Financial support for this study was provided by the Intermountain Region of the Forest Service, U.S. Department of Agriculture, in cooperation with the Intermountain Forest and Range Experiment Station, Ogden, Utah. Enhancing the manuscript were the helpful reviews by Dr. Minoru Hironaka and Prof. Frederic D. Johnson, University of Idaho; Dr. Dorothy Douglas, Boise State University; Dr. James Habeck, University of Montana; Dr. Stephen Arno, Dr. Walt Mueggler, and Ronalk Mauk, Intermountain Forest and Range Experiment Station; and two anonymous reviewers.

Literature Cited

Arno, S. F., and D. G. Simmerman. 1982. Forest Succession of Four Habitat Types in Western Montana. Review draft, 129 p. Intermtn. For. and Range Exp. Stn., Ogden, Utah.

Braun-Blanquet, J. 1932. Plant Sociology; The Study of Plant Communities. (English Trans, by G. D. Fuller and H. S. Conard. McGraw-Hill, New York.

Cattelino, P. J., I. R. Noble, R. O. Slatyer, and S. R. Kessell. 1979. Predicting the multiple pathways of plant succession. Environmental Management 3(1): 41-50.

Daubenmire, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22: 301-330.

———, and J. B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Wash. Agric. Exp. Stn., Tech. Bull. 60. Pullman, Wash.

Eyre, F. H. (ed.). 1980. Forest Cover Types of the United States and Canada. Society of America Foresters, 5400 Grosvenor Lane, Wash., D.C.
Gleason, H. A. 1927. Further views on the succession-concept. Ecology 8(3): 299-326.
Henderson, J. A., and N. E. West. 1977. ECOSYM- vegetation classification. Dept. of Forestry and Outdoor Rec. Utah State Univ., Logan, Utah.
Huschle G., and M. Hironaka. 1980. Classification and ordination of seral plant communities. J. Range Mgt. 33(3): 179-182.
Krajina, V. J. 1965. Biogeoclimatic zones and biogeocoenoses of British Columbia, pp. 1-17 *in*: Ecology of Western North America. Univ. of British Columbia.
Kuchler, A. W. 1966. Potential natural vegetation of the United States, including Alaska and Hawaii, pp. 89-92 *in*: National Atlas of the United States. USDI Geol. Survey, Washington, D.C.
Layser, E. F. 1974. Vegetation classification: its application to forestry in the northern Rocky Mountains. J. For. 72: 354-357.
Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, Inc., New York.
Noble, I. R., and R. O. Slatyer, 1977. Post-fire succession of plants in Mediterranean ecosystems, pp. 27-36 *in*: Proc. of Symp. on Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA For. Serv. Gen. Tech, Rep. WO-3.
———. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurring disturbance. Vegetatio 43: 5-21.
Pfister, R. P. 1977. Ecological classification of forest land in Idaho and Montana, pp. 329-358 *in*: Proc. of Ecological Classification of Forest Land in Canada and Northwestern U.S.A. Univ. of British Columbia.
Pfister, R. D., and S. F. Arno. 1980. Classifying forest habitat types based on potential climax vegetation. For. Sci. 26(1): 52-70.
———, B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest Habitat Types of Montana, USDA For. Serv. Gen. Tech, Rep. INT-34. Intermtn. For. and Range Exp. Stn., Ogden, Utah.
Shimwell, D. W. 1971. The Description and Classification of Vegetation. Univ. of Wash. Press, Seattle.
Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittams. 1981. Forest Habitat Types of Central Idaho. USDA For. Serv. Gen. Tech. Rep. INT-114. Intermtn. For. and Range Exp. Stn., Ogden, Utah.
West, D. C., H. H. Shugart, and D. B. Botkins (ed.). 1981. Forest Succession Concepts and Application. Springer-Verlag, New York.

Received September 23, 1982
Accepted for publication April 4, 1983

Ruth Wilson-Jacobs[1]

Cooperative Wildlife Research Unit
Oregon State University
Corvallis, Oregon 97331

and

E. Charles Meslow

Cooperative Wildlife Research Unit
Oregon State University
Corvallis, Oregon 97331

Distribution, Abundance, and Nesting Characteristics of Snowy Plovers on the Oregon Coast[2]

Abstract

Distribution, abundance, and nesting characteristics of Snowy Plovers (*Charadrius alexandrinus*) were studied on the Oregon coast during 1978 and 1979. A maximum of 100 adults and fledged juveniles were observed on 12 discrete beach segments. Of 72 nests observed, at least 19 were lost to corvid predation, 11 were destroyed by storms and moving sand, and 9 were successful. Nest sites were characterized as flat areas with sand substrate and an average of 26 percent driftwood and less than 1 percent live vegetation for cover.

Introduction

As early as 1929 Bent (1929: 248) suspected that human developments on the Pacific coast encroached on habitat of Snowy Plovers (*Charadrius alexandrinus*). On the Oregon coast, information on distribution and abundance of Snowy Plovers before the 1970s was qualitative (Gabrielson and Jewett 1940: 246) and insufficient for an analysis of the influences of human developments on Snowy Plovers. Infrequent survey data from 1972 through 1977 led observers to suspect that numbers of Snowy Plovers were declining (W. Hoffman, unpubl. data; Oregon Dept. Fish and Wildl., unpubl. data), but variability in timing and thoroughness of surveys prohibited use of the data to investigate changes in distribution and abundance. Stabilization of sand with European beachgrass (*Ammophila arenaria*) (Cooper 1958, Wiedemann 1966), increased levels of recreational activity (USDA 1977), and community and industrial developments were suspected to be detrimental to Snowy Plovers (W. Hoffman, pers. comm.; Marshall 1969). Choice by Snowy Plovers of flat, unvegetated nesting habitat (Bent 1929: 248) and the month-long period required for chicks to fledge (Boyd 1972) were the basis for suspicions that nesting activities were most susceptible to human influences. The purpose of the present study was to establish baseline data for Snowy Plovers on the Oregon coast. Specific objectives were to (1) describe distribution and abundance patterns

[1]Present address: 140 Cliffside Dr., Grants Pass, Oregon 97527.

[2]Study conducted under the auspices of the Oregon Cooperative Wildlife Research Unit: Oregon Department of Fish and Wildlife, Oregon State University, U.S. Fish and Wildlife Service, and Wildlife Management Institute cooperating. Oregon State University Agricultural Experiment Station Technical Paper No. 6173.

during the breeding season, (2) document nesting phenology, (3) study nest success, and (4) describe nesting habitat.

Methods

Distribution and abundance of Snowy Plovers were evaluated with two surveys (on foot) of sand beaches during 23 April to 23 June 1978 and 11 May to 20 June 1979. Beaches were selected based on historical records of use by Snowy Plovers and similarity to beaches with present use; about 240 km of beaches met these criteria (Fig. 1). In 1979 an additional 50 to 60 km of beach were surveyed to ensure adequate coverage, notably areas with dredge spoil on the interior of the North Spit Coos Bay. Timing of surveys followed a recommendation by G. Page (Point Reyes Bird Observatory, pers. comm.) that the best time to estimate numbers of breeding adults was in May and June. This was considered the period after migration from coastal wintering grounds of adults that bred elsewhere, yet before an influx of fledged juveniles from other areas.

We assessed seasonal changes in abundance, nesting activities, and nesting habitat at four study areas on the central Oregon coast (Sutton Creek, Siltcoos River, and Tahkenitch River outlets, and South Beach at Yaquina Bay; Fig. 1). Preliminary observations indicated high levels of recreational activity at South Beach, intermediate levels at Sutton and Siltcoos, and virtually no activity at Tahkenitch.

Nests were located by searching each study area at least weekly between 0600 and 1100 from 1 April to 10 August 1978 and 17 March to 31 July 1979. Additional searches occurred infrequently in March 1978 and August 1979. Simultaneous surveys were made to assess abundance of Snowy Plovers. Nests were visited at intervals varying from 1 to 6 days during 1978. In 1979, nests were visited at Sutton, Siltcoos, and Tahkenitch on a daily basis and at 1- to 4-day intervals at South Beach. Once a clutch was complete (three eggs or the onset of incubation), observer activity at nests was reduced by observing nests from a distance, unless a nest was vacant or eggs were not visible. Nineteen adults were captured with drop-traps (Boyd 1972) and noose snares (G. Page, pers. comm.) and banded before the 1979 nesting season.

After hatching or loss of eggs, we measured cover characteristics at each nest site (20 m radius of the nest) and at a paired site selected randomly within 75 m of each nest (referred to as random site) using line intercept sampling (Canfield 1941). We extended 6 20-m transects at 60 degree intervals from the nest and center of each random site and measured cm of driftwood, *A. arenaria*, total live vegetation (including *A. arenaria*), and total cover (all previous components plus dead vegetation and miscellaneous debris) intercepted by the transects. Measurements on the transects were recorded in segments of 0-0.5, 0-1.0, 0-1.5, 0-2.0, and 0-20 m from centers of the sites. An additional estimate of cover was made with square meter plots centered over nest and random sites. On line transects, cover estimates with 0.5 m of the sites showed greatest dissimilarity among nest sites and random sites and were most similar to cover estimates from square meter plots. Therefore, only measurements on transects within 0.5 m of the sites were further considered. Cover estimates for driftwood and live *A. arenaria* (the predominant nonliving and living cover components) were used to test for differences in characteristics of nest sites and random sites. Statistical analyses were completed before converting data to a measure of percentage cover.

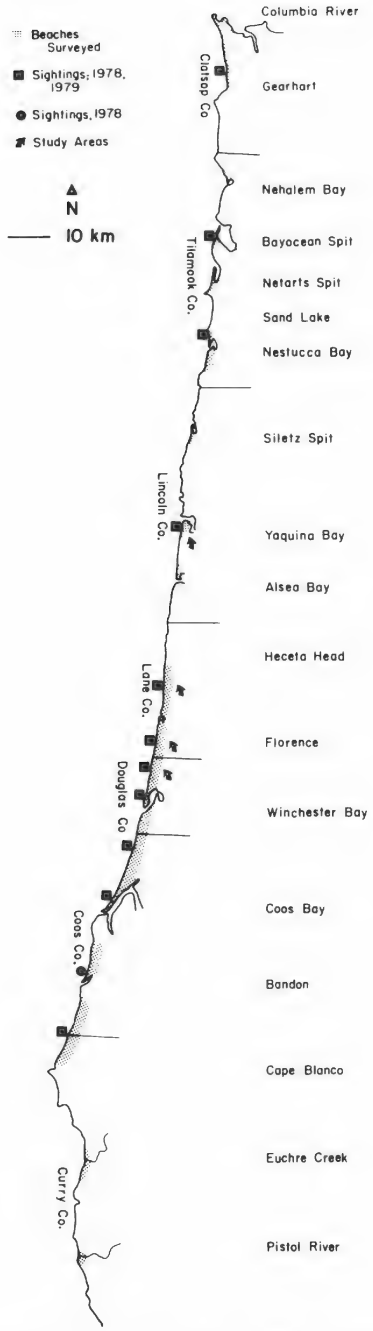

Figure 1. Beaches surveyed during 1978 and 1979 for Snowy Plovers and locations of study areas.

All statistical analyses followed Sokal and Rholf (1969). Tests are reported with results.

Results and Discussion

The Snowy Plover was neither abundant nor widely distributed along the Oregon coast during the breeding season. A maximum of 100 adults and fledged juveniles were observed during the two coastal surveys on 12 discrete beach segments (Table 1).

TABLE 1. Observations of Snowy Plovers along the Oregon coast during surveys in 1978 and 1979.

Beaches Surveyed	Dates of Surveys 1978	1979	Number 1978	1979
Peter Iredale St. Pk. to Gearhart	31 May	7 June	4	4
Bayocean Spit	2 June	9 June	21	7
Sand Lake	19 May	10 June	5	3
N. Spit Umpqua R.	23 April	8 June	10	4
Tenmile Creek	12 May	21 May	7	2
N. of Coquille R.	21 June	16 June	7	0
N. of Floras Lake	22-23 June	17-18 June	22	23
South Beach	[a]	[a]	2	3
Sutton Creek	[a]	[a]	6	6
Siltcoos River	[a]	[a]	5	2
Tahkenitch River	[a]	[a]	1	1
N. Spit Coos Bay[b]	5 May	20 June	3	45
Totals	—	—	93	100

[a]Numbers of birds were calculated from data from weekly surveys in June.
[b]Only beaches, not dredge deposits, associated with the spit were surveyed in 1978. Because Snowy Plovers were found on the dredge deposits in 1979, we believe the observation of 3 birds underestimates use of the spit in 1978.

Because the age of flying individuals could not be determined, adults and fledged juveniles were grouped; the majority of these individuals were probably adults because less than 6 percent of individuals positively identified were fledged juveniles.

We believed that the total number of birds recorded in 1978 was low because of incomplete coverage of portions of the North Spit Coos Bay. Totals for the other beaches were relatively consistent between the 2 years. Areas with previous records of use during the breeding season (March through August) where Snowy Plovers were not observed during either the 1978 or 1979 surveys were Clatsop, Nehalem, Netarts, Nestucca, Siletz, Alsea, and Pistol River spits, Neskowin Beach, and Euchre Creek (Gabrielson and Jewett 1940 : 246; Oregon Dept. Fish and Wildl., unpubl. summary of sighting records).

Because 1978 and 1979 were the first years that complete coastal surveys were conducted in the spring, assessing changes in abundance over years for the entire coast seemed impractical. Surveys in August and September at South Beach, the single area on the coast with relatively comparable survey records over time, indicated a steady decline in abundance from 1967 to 1979 (year and number of birds, respectively: 1967, 25; 1968, 35; 1969, 25; 1971, 15; 1972, 13; 1977, 10; 1978, 1; 1979, 0; W. Hoffman and Oregon Dept. Fish and Wildl., unpubl. data; Wilson 1980).

Developments that influenced South Beach during that time included opening of a state park adjacent to the beach and provision of vehicle access to the beach from the bordering jetty. The apparent absence of birds from nine of the 21 beach segments with historical records of use indicated to us that distribution was more restricted now

than previously. An adult Snowy Plover and nest were found, however, at Euchre Creek (J. Collins, Oregon Dept. Fish and Wildl., pers. comm.) in April 1979, before the coastal survey when no birds were observed. Therefore, 2 years of survey data did not absolutely demonstrate presence or absence of breeding birds from coastal areas.

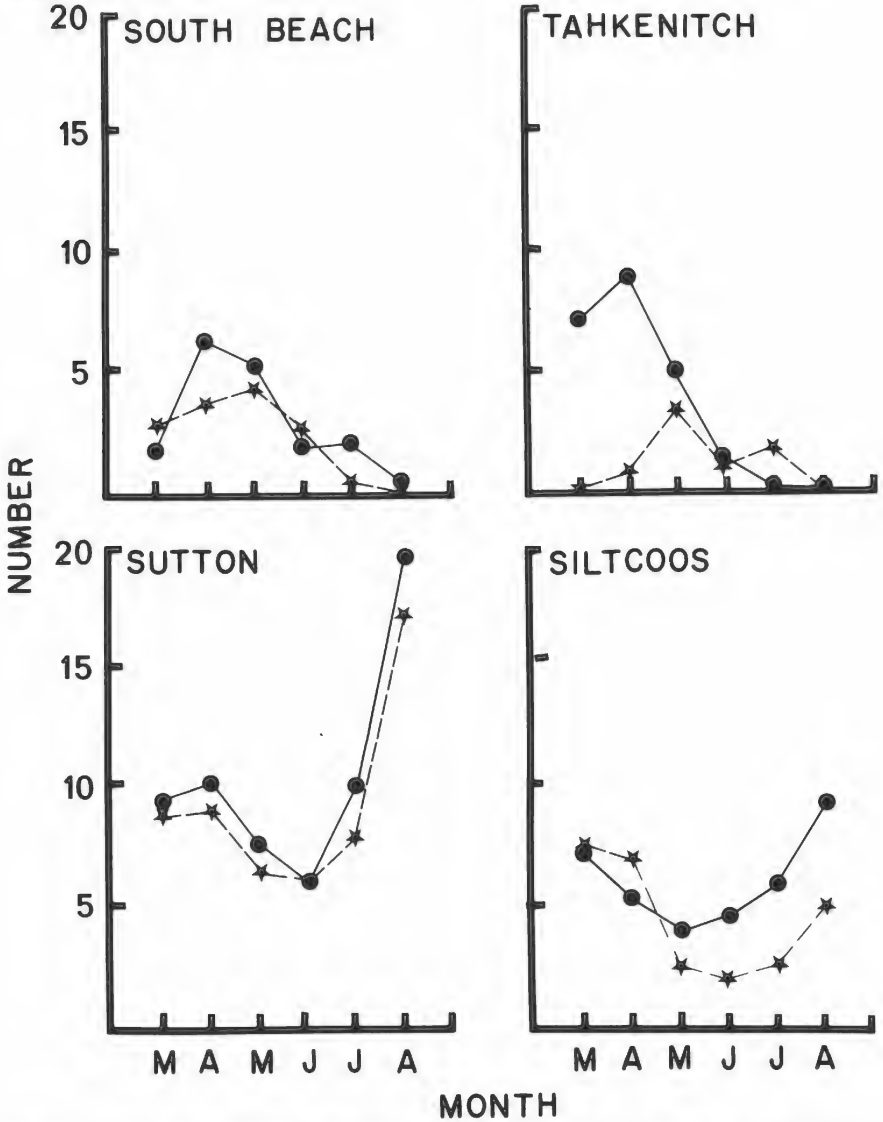

Figure 2. Mean monthly survey observations of adults based on weekly surveys at South Beach, Sutton, Siltcoos, and Tahkenitch study areas; 1978 (solid line), 1979 (dashed line); March to August. Differences in abundance were significant between areas ($p < 0.005$) but not between months ($p > 0.25$, ANOVA). Sutton supported the highest number ($p < 0.05$, Newman-Keuls).

Differences were not significant in abundance of Snowy Plovers among months of the breeding season based on weekly surveys of study areas ($p > 0.25$, ANOVA; Fig. 2). We observed consistent trends in abundance, however, between 1978 and 1979 at Siltcoos and Sutton that corresponded to trends observed on the California coast (Page *et al.* 1979). Numbers of adults declined from March and April to May and June, followed by an increase through the remainder of the sampling period. This trend corresponded to the explanation given earlier for movements of adults and juveniles. The trend of a decrease in numbers of adults at South Beach and Tahkenitch from April and May through the sampling period probably reflected a flocking tendency following the peak of breeding activities because we observed adults with bands move from one study area to another.

Nesting Phenology and Nest Success

The Snowy Plover was a persistent nester over a long nesting season but had low nest success. Seventy-two nests were found on the study areas (48 in 1978 and 24 in 1979, Table 2). We estimated the earliest onset of nesting activities as mid-March (1978); the latest nest observed was extrapolated to hatch in mid-August (also 1978, Fig. 3). Nest initiation was most frequent in April and May (31 and 32 percent, respectively, of all nests).

TABLE 2. Measures of Snowy Plover nest success at 4 study areas on the Oregon coast, 1978 and 1979.

	South Beach		Sutton		Siltcoos		Tahkenitch	
	1978	1979	1978	1979	1978	1979	1978	1979
No. Nests	8	2	14	11	15	7	11	4
No. Successful Nests	4	2	1	0	1	0	0	1
Fates of Unsuccessful Nests[a]	0-0-0	0-0-0	3-5-0	2-2-1	5-3-0	4-1-1	2-0-1	3-0-0

[a]Listed in order of number of nests known lost to corvids, destroyed by rain storms or moving sands, or abandoned.

Average nest success (the proportion of nests with at least one egg hatching) was 13 percent for both years. Highest success, but the fewest nests, were found at South Beach, the area with the highest level of recreational use (Wilson 1980). Predation by the American Crow (*Corvus brachyrhynchos*) and Northern Raven (*C. corax*) and movement of sand were important in nest loss (at least 30 percent of all losses resulted from corvid predation and 16 percent were attributed to movement of sand, Table 2). Nest loss associated with sand movement generally occurred when wind-driven sand buried eggs or moved eggs from nest scrapes. Cause of nest failure of 30 nests was not determined because rain or blowing sand removed evidence. These nest losses were not attributable to weather because we searched for, but did not find, buried eggs or eggs damaged by rain or hail. Because predators other than corvids were never implicated in nest loss, we believed corvids were primarily responsible for the loss of these nests.

Our observations indicated a high incidence of renesting, but the frequency could not be estimated because of movements of adults among study areas. As examples, in 1979 a pair at Sutton made at least three nesting attempts and a pair at Siltcoos made at least two attempts. A female nested unsuccessfully at least twice with a mate at Siltcoos, moved to Sutton for a third attempt following death of her first mate, and returned to Siltcoos for a fourth attempt with a third mate. Her final mate was involved in at least two earlier nesting attempts.

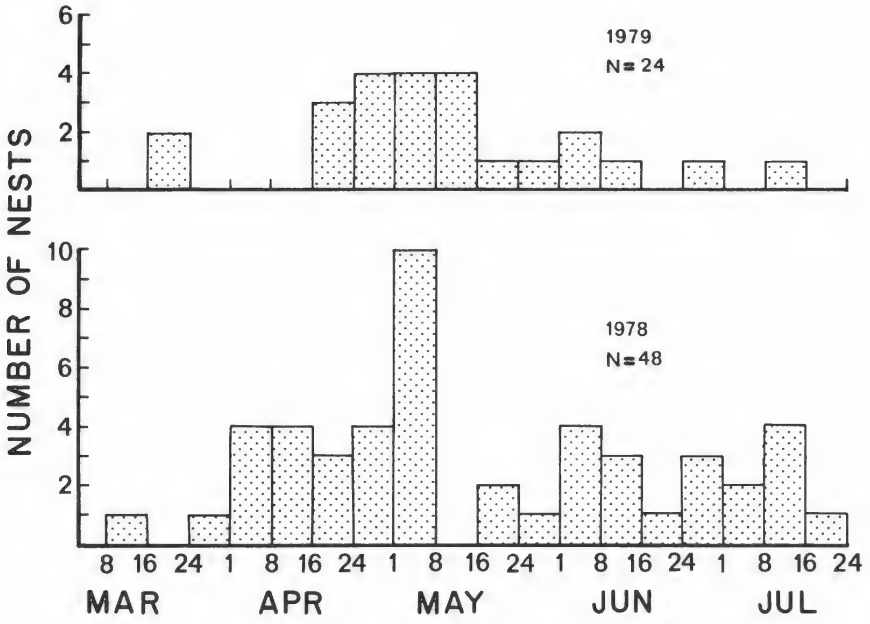

Figure 3. Estimated dates of Snowy Plover nest initiation for nests found at South Beach, Sutton, Siltcoos, and Tahkenitch study areas.

The level of nest success observed in our study was low compared with levels documented by others. In the Great Plains, Boyd (1972) and Grover (1979) reported levels from 37 to 73 percent. G. Page (pers. comm.) observed from 25 to 85 percent nest success at coastal and interior locations in California. Nest loss has been associated with avian and mammalian predation [predators include California Gulls (*Larus californicus*), Northern Ravens, American Crows, coyotes (*Canis latrens*), skunks (*Mephitis*), and racoons (*Procyon lotor*)], weather conditions (including storm tides, wind-driven sand, and hail or rain storms), cattle stepping on eggs, and human disturbance (Boyd 1972; Grover 1979; G. Page, pers. comm.; Rittinghaus 1975). Seemingly, the majority of factors causing nest loss are factors with which Snowy Plovers have evolved. And, healthy populations should be adapted to survive the losses unless predation pressures are more intense now than in the past, or the bird's ability to withstand high levels of nest loss has diminished because of other factors influencing the bird.

Conceivably Snowy Plovers that nest on the Oregon coast experience low nest

TABLE 3. Percent cover of driftwood, **Ammophila arenaria**, live vegetation, and total cover of Snowy Plover nest sites and paired random sites. N = 65.

	Nest Site		Random Site	
	Mean	S.E.	Mean	S.E.
Driftwood	26.0	3.0	5.0	1.0
A. arenaria	0.5	0.2	0.2	0.1
Live Vegetation	0.9	0.3	0.4	0.1
Total Cover	28.0	3.0	5.0	1.0

success because these birds are breeding on the periphery of their coastal range, and habitat conditions are not optimal. Yet, Widrig (1980) observed 60 to 80 percent nest success at Leadbetter Point, Washington, a location that approaches the northernmost extent of the Snowy Plover's breeding range.

Shorebirds as a group have wide distributions (Pitelka 1979); frequently use multiple-nesting strategies (Jenni 1974), which is an adaptation associated with unstable habitats (Emlen and Oring 1977, Orians 1969); and have relatively high rates of adult survival (45 to 85 percent per year; Boyd 1962, Lack 1954: 92). The Killdeer (*Charadruis vociferous*), a congener of the Snowy Plover, commonly inhabits areas influenced by human activity. These features of charadriiforms confound interpretation of the importance of two seasons of low nest success on the overall status of Snowy Plovers on the Oregon coast. We reserve judgment until additional information is available on reproductive success, survival of adults and juveniles, and movements of birds among breeding populations. But, we caution that conservative attitudes are appropriate relative to alteration of nesting habitat by man.

Nest Site Characteristics

Sixty-five nest sites and paired random sites were analyzed to determine cover characteristics of nest sites; seven sets of sites were excluded because of alteration before measurement. Mean cover of nest sites was 28 percent (Table 3). Driftwood constituted the vast majority of the cover (26 percent), and live vegetation accounted for less than 1 percent. *A. arenaria* accounted for more than half of the vegetation in the vicinity of nest sites. Estimates of cover of driftwood and *A. arenaria* were similar among the four study areas for nest sites and for random sites ($p > 0.05$, MANOVA), but cover at nest versus random sites was dissimilar ($p < 0.05$, MANOVA). Nest sites had more cover (28 percent for nests versus 5 percent for random sites); the apparent preference for more cover than was present on the average was usually satisfied by nesting near driftwood, and only rarely, by nesting close to vegetation.

Since the amount of dense vegetation on the Oregon coast has dramatically increased with introduction of *A. arenaria* (Wiedemann 1966), and since dense vegetation was not selected by Snowy Plovers for nesting habitat, speculation that the introduction of *A. arenaria* has restricted distribution of nesting Snowy Plovers seems valid. Changes in distribution of the Least Tern (*Sterna albifrons*) (Massey 1974), and Piping Plover (*Charadrius melodus*) (Wilcox 1959), species which also nest on sandy beaches, were associated with changes in vegetation cover. Likely consequences of restricted distribution of a population are reduced abundance or increased population influence by local factors or both. Possibly, therefore, the presence of *A. arenaria* has indirectly affected abundance of Snowy Plovers by influencing distribution.

Conclusions

The information presented in this paper can serve only as preliminary data for an assessment of the status of Snowy Plovers on the Oregon coast. Information on abundance, mixing of interior and coastal populations, and levels of reproductive success over several years is essential for an accurate assessment. Concern for the Snowy Plover is appropriate because of low abundance and restricted distribution. The appropriate expression of that concern should be additional monitoring of population performance

and, until additional information is available, reducing and possibly reversing unnatural changes on areas used by the birds.

Acknowledgments

We thank J. Crawford, S. Jacobs, W. Krueger, and G. Page for helpful discussions during this research. R. Deering, M. Schnoes, and J. Shay assisted in data collection. The research was supported by the Oregon-Washington Interagency Wildlife Committee and funded by the Bureau of Land Management, Oregon Department of Fish and Wildlife, U.S. Army Corps of Engineers, U.S. Forest Service, and U.S. Fish and Wildlife Service.

Literature Cited

Bent, A. C. 1929. Life histories of North American Shorebirds. U.S. Natl. Mus. Bull. 146: 246-252.

Boyd, H. 1962. Mortality and fertility of European charadrii. Ibis 104: 368-387.

Boyd, R. L. 1972. Breeding Biology of the Snowy Plover at Cheyenne Bottoms Waterfowl Management Area, Barton County, Kansas. M.S. thesis, Kansas State Teachers College, Emporia.

Canfield, R. 1941. Application of the line interception method in sampling range vegetation. J. For. 39: 388-394.

Cooper, W. S. 1958. Coastal Sand Dunes of Washington and Oregon. Geol. Soc. Am. Mem. 72, Baltimore, Waverly Press.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215-223.

Gabrielson, I. N., and S. G. Jewett. 1940. Birds of Oregon. Oregon State College, Corvallis.

Grover, P. B. 1979. Habitat Requirements of Charadriiform Birds Nesting on Salt Flats at Salt Plains National Wildlife Refuge. M.S. thesis, Oklahoma State Univ., Stillwater.

Jenni, D. A. 1974. Evolution of polyandry in birds. Amer. Zool. 14: 129-144.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford, Clarendon Press, London.

Massey, B. W. 1974. Breeding biology of the California least tern. Proc. Linnean Soc., New York. 72: 1-24.

Marshall, D. B. 1969. Endangered Plants and Animals of Oregon, III: Birds. Spec. Rep. 278, Agric. Exp. Sta., Oregon State University, Corvallis.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589-603.

Page, G. W., L. E. Stenzel, and C. M. Wolfe. 1979. Aspects of the occurrence of shorebirds on a central California estuary. Stud. in Avian Biol. 2: 15-32.

Pitelka, F. A. 1979. The Pacific coast shorebird scene. Stud. in Avian Biol. 2: 1-11.

Rittinghaus, H. 1975. Der seeregnepfeifer, mit beitragen von Jacob Walters, *in*: U. N. Glutz von Blotzheim, K. M. Bauer, and E. Bessel, eds. Handbuch der vogel milteleuropas, Band 6, Caradriiformes. Akademische Verlagsgesellschaft, Wiesbaden. (partial translation by F. Lanting).

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman Co., San Francisco.

U.S. Department of Agriculture. 1977. Final Environmental Statement, Oregon Dunes National Recreation Area, Management Plan. U.S. For. Serv., Pac. Northwest Reg.

Wiedemann, A. M. 1966. Contributions to the Plant Ecology of the Oregon Coastal Sand Dunes. Ph.D. thesis, Oregon State Univ., Corvallis.

Widrig, R. 1980. Snowy Plovers at Leadbetter Point: An Opportunity for Wildlife Management? U.S. Fish Wildl. Serv., Willapa Natl. Wildl. Refuge, Ilwaco, Washington.

Wilcox, L. 1959. A twenty year banding study of the piping plover. Auk 76: 129-152.

Wilson, R. W. 1980. Snowy Plover Nesting Ecology on the Oregon Coast. M.S. thesis, Oregon State Univ., Corvallis.

Received March 5, 1982
Accepted for publication August 25, 1982

David L. Nelson

and

Patti L. Schuttler

Intermountain Forest and Range
Experiment Station
507 25th Street
Ogden, Utah 84401

Histology of Cowania stansburiana Actinorhizae

Abstract

Actinorhizae of *Cowania stansburiana* are indeterminate, dichotomously branching, modified roots that form coralloid nodule clusters typical of those on other Rosaceae. An individual nodule lobe possesses a meristematic zone, enlarged endophytic cortical cells, a stele, and a poorly defined periderm. The endophyte thallus is filamentous ca. 0.5 μm diameter; no septa were discerned. The endophyte invades immediately proximal to the meristem, first stimulating enlargement of the host nucleus, then cell enlargement. Initially the endophyte is closely associated with the nucleus, then the conoly expands to fill enlarging cortical cells. Obpyriform vesicules ca. 2 x 3 μm form on the colony periphery and are present during the primary endophyte phase. Abundant amyloplasts are present in adjoining cells during this phase. Vesicles, hyphae, and host nuclei then degenerate and disappear. No other endophyte phases were observed. Zones of sloughing periderm cells exposed degenerating endophyte cells and may serve as a mechanism for endophyte propagule release.

Introduction

Many members of the Western United States wildland shrub community in the Rosaceae are of special practical value on wildlife and livestock ranges and in vegetative reclamation (Plummer *et al.* 1968, Blauer *et al.* 1975, Monsen 1975). Six genera of rosaceous shrubs, including Stansbury cliffrose (*Cowania stansburiana* Torr.), are known to form symbiotic nitrogen-fixing associations with *Frankia* Brunchorst (Actinomycetales) (Becking 1970), as reviewed by Nelson (1983). The endosymbiont of all these genera except *Cowania* have been studied to some extent. A description of *Cowania* actinorhizae would give a more complete knowledge for the Rosaceae.

Morphological and histological descriptions have been made of actinorhizae and the endophyte for *Dryas drummondii* (Lawrence *et al.* 1967), *Cercocarpus montanus* (Hoeppel and Wollum 1971), and *Purshia tridentata* (Krebill and Muir 1974, Bond 1976a). Bond (1976a) briefly examined the fine structure. Righetti and Munns (1980) noted (but published no description of) a nodule-endophyte structure in *Cowania stansburiana* similar to that reported by Krebill and Muir (1974) for *Purshia tridentata*. Nodules formed in the Rosaceae appear to be perennial in nature with an indeterminate, generally dichotomous branching that eventually develops into coralloid nodule clusters up to several centimeters diameter. As with other actinorhizal families, nodule anatomy resembles that of a primary root, except there are few or no root hairs, no root cap, and a superficial periderm rather than epidermis. The stele is central and not invaded by the endophyte.

Endophyte colonies occur in hypertrophied parenchyma cells in a narrow zone in the central to outer cortex. In nonrosaceous genera, these cells tend to be located through-

out the cortex (Bond 1974, 1976b). Endophyte colonies consist of a filamentous mat of fine hyphae characteristic of actinomycetes. Bond (1976a) for *Purshia*, and Hoeppel and Wollum (1971) for *Cercocarpus*, describe an endophyte with septate hyphae. Other endophyte structures, such as granulated bodies or bacteroides (van Dijk and Merkus, 1976), were found in the *Purshia* endophyte by Bond (1976a) but not by Krebill and Muir (1974). Lawrence *et al.* (1976) found granule-containing cells in the *Dryas* endophyte that he considered comparable to the bacteroides of other endophytes.

Methods and Materials

Nodules were collected for histological study from Stansbury cliffrose plants from Kyle Canyon in southern Nevada. Actively growing nodules were selected, washed with water, divided into individual nodule lobes, and fixed with FAA after Sass (1961). The tertiary butyl-alcohol paraffin-oil method of dehydration and paraffin infiltration of Johansen (1940) was used to prepare material for sectioning. Serial transverse and longitudinal sections of entire nodule lobes were made at 10-12 μm with a Leitz rotary microtome. The orseillin BB-aniline blue staining technique of Peterson and Shurtleff (1965) was then used to differentiate tissues for examination using a Nikon Optiphot compound light microscope. Twelve sectioned nodule lobes were used for the analysis. Dimensions and distances represent an average from a detailed analysis of serial sections (five nodule lobes sectioned transversely and two longitudinally).

Results

The following account of *Cowania* root nodule-endophyte histology and development proceeds in a proximal direction beginning at the nodule lobe tip. Anatomically, the nodule lobes were root-like, but no typical root cap, root hairs, or epidermis were present. A periderm-like zone four to five cells thick (55-60 μm across) shielded a loosely organized meristematic zone. The widest central portion of the meristematic zone extended 60 μm to the first recognizable stele containing vessels with annular and spiral wall thickenings. The first evidence of endophyte activity was noted in parenchyma cells in the cortical zone immediately proximal to the meristematic zone. The nuclei of scattered cells were enlarged two to two and a half times the diameter of other cells. This enlargement was in a zone 80-100 μm proximal to the nodule tip prior to any noticeable cell enlargement. Then, for another 50 μm, enlargement of cells with the enlarged nuclei was detected before any endophyte hyphae were resolved. The first hyphae noticed were closely associated with the host nucleus (Fig. 1). In a zone extending to 480 μm proximal, hyphae enveloped the nucleus, and then the endophyte colony expanded from the nuclear envelopment to completely fill host cells. Cells containing endophyte colonies hypertrophied to a size roughly 25-95 μm by 60-150 μm. Cells tended to be enlarged the most in a radial plane. Intercellular extension of hyphae, even in the invasion zone near the meristem, was not resolved by our stain technique and light microscopy, nor was a presence of hyphal septa. Hyphae were 0.5-1 μm in diameter in endophyte colonies, although there was uncertainty concerning the true diameter because of their tightly matted nature. Vesicles were first present at the 480 μm position proximal to the nodule tip.

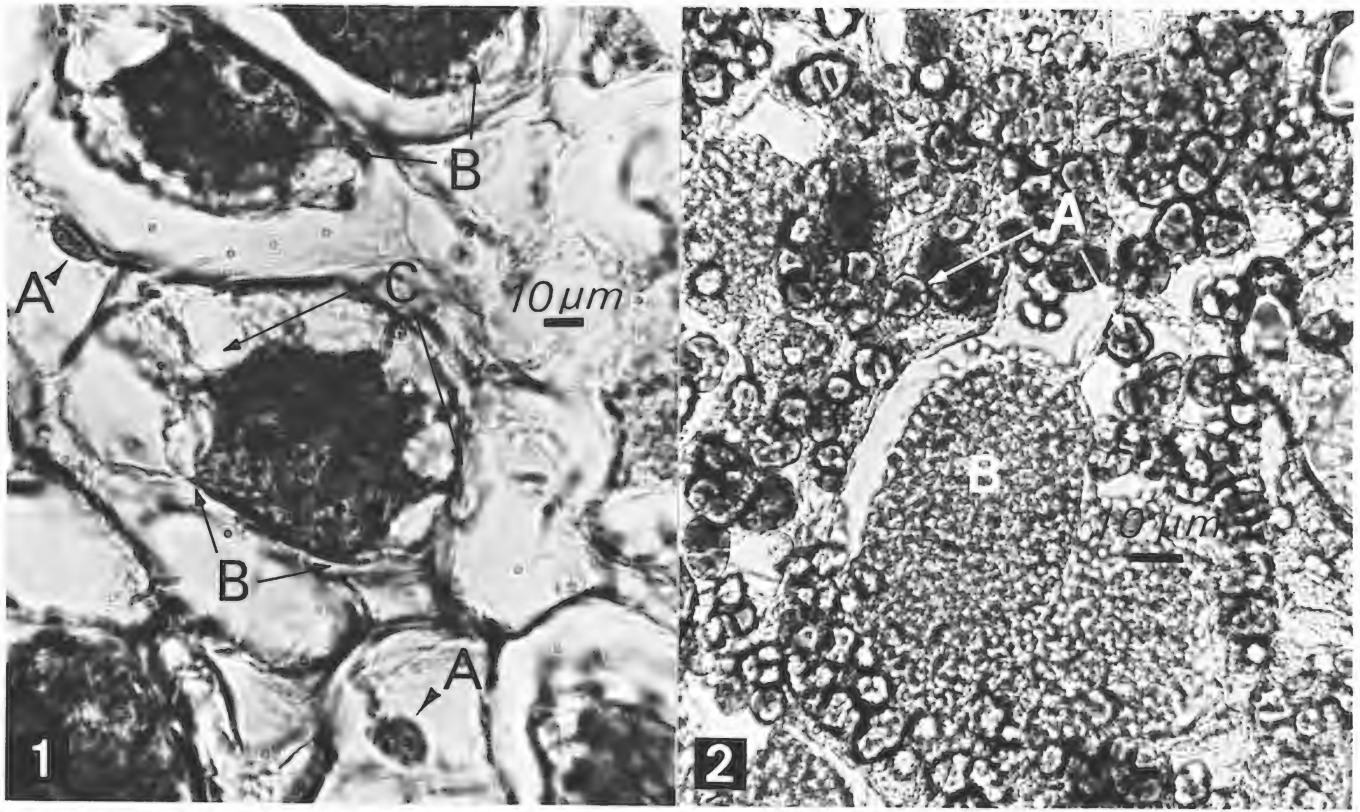

Figure 1. Transverse section of cortical cells 150 µm proximal to nodule tip. Note size of nuclei in unaffected cells (A); compared to invaded cells (B); endophyte hyphae have almost enveloped the enlarged host nuclei (C). Figure 2. Transverse section showing numerous amyloplasts (A) in cortical parenchyma cells surrounding vesicle cells (B).

Amyloplasts were first present at 500 μm in parenchyma cells that were surrounding the endophyte vesicle cells (Fig. 2). Host nuclei in the endophyte cells were enlarged three to five times the diameter of nuclei in adjacent cells and were strikingly hyperplastic. At 960 μm proximal, vesicle development was at maximum. The endophyte invaded host cells were limited to a zone in the medial to outer cortex and were, in most cases, separated from each other by parenchyma one or more cells across (Fig. 3). Vesicles were terminal on hyphae and nearly all were located on the colony periphery (Fig. 4). Vesicles averaged 2 x 3 μm in a plane parallel to the attached hyphae and were obovate to obpyriform in shape. In the zone of full vesicle development, the endophyte colonies appeared to shrink, leaving a space between the vesicles and host cell wall (Fig. 4). Degenerating endophyte colonies were first present at 1.2 mm proximal to the nodule tip, and this continued until only a few or no colonies were present at 1.9 mm. First, vesicles and host nucleus were no longer present, and then the hyphal mass appeared to shrink away until no resolvable trace was left. As the endophyte colony declined, the host cell decreased in volume. The diameter of the nodule lobe also was reduced, until at the proximal end, it was about two-thirds the maximum. With degeneration and disappearance of the endophyte-vesicile colonies, amyloplasts also disappeared from surrounding parenchyma cells until at the proximal end of the nodule lobe none were present. No other endophytic structures (such as granulae, bacteroides, or sporangia) reported elsewhere were found.

Exterior to the cortex was a poorly defined periderm-like zone. Inner derivatives, perhaps phelloderm, became filled with a dark staining material; outer derivatives, perhaps phellem, became shrunken and, as the nodule diameter increased, split irregularly to form the mosaic of rust-brown patches seen in surface view (Fig. 5). Toward the proximal end of the nodule, there were zones where the periderm sloughed away entirely, exposing degenerating cortical tissue (Fig. 6).

The stele appeared normal, with no evidence of cell enlargement or endophyte hyphae. No secondary growth occurred in the stele through the nodule lobe area described. No examination was made in branches proximal to this area. At the approximate position where endophyte colonies began to decline, a dark staining material, possibly tannin, appeared in endodermal cells. The amount of each cell lumen and number of cells containing the substance increased until, at the proximal end of the lobe, almost all cells appeared filled.

Discussion and Conclusions

The histology of *Cowania* nodules and endophyte observed in this study conformed with that reported for other genera of the Rosaceae. No hyphal septa were found nor hyphae observed in host tissue outside the vesicle-colony cells. Similarity in form of endophyte hyphae, vesicle colonies, and nodule structure places the *Cowania* endophyte in the genus *Frankia*, which is the generally accepted taxon for the endophytes of actinomycete-induced nodules. Form and size of the *Cowania* endophyte, like those found in other rosaceous genera, are variable. Reports of size and shape of endophyte hyphae and vesicles, respectively, are in *Dryas drummondii* (1.4-1.9 μm) and (2-5 μm, round to oval) (Lawrence *et al.* 1967); in *Dryas* sp. (0.5-0.89 μm) and (1.2-2.0 x 1.5-2.0 μm) (Becking 1977a); in *Cercocarpus montanus* and *C. paucidentatus* (0.5

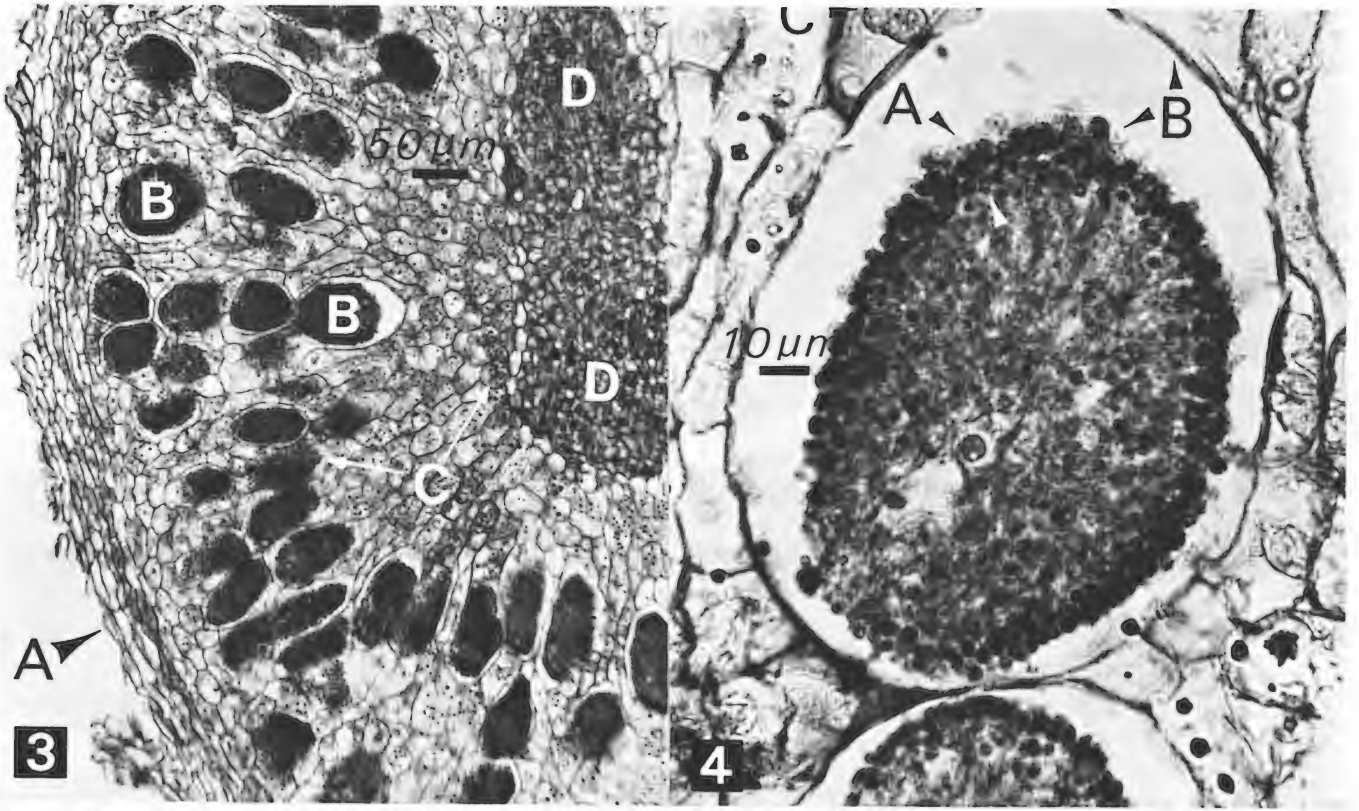

Figure 3. Transverse section in the mid vesicle-colony zone. Note outer periderm-like zone (A); vesicle colonies (dark-colored bodies) in outer cortex (B); nonendophyte inner cortex (C); and stele with two vascular traces (D). Figure 4. Transverse section of a vesicle colony. Note zone of vesicles on periphery of colony (A); space between vesicles and host cell wall (B); and amyloplasts in surrounding cortical parenchyma cells (C).

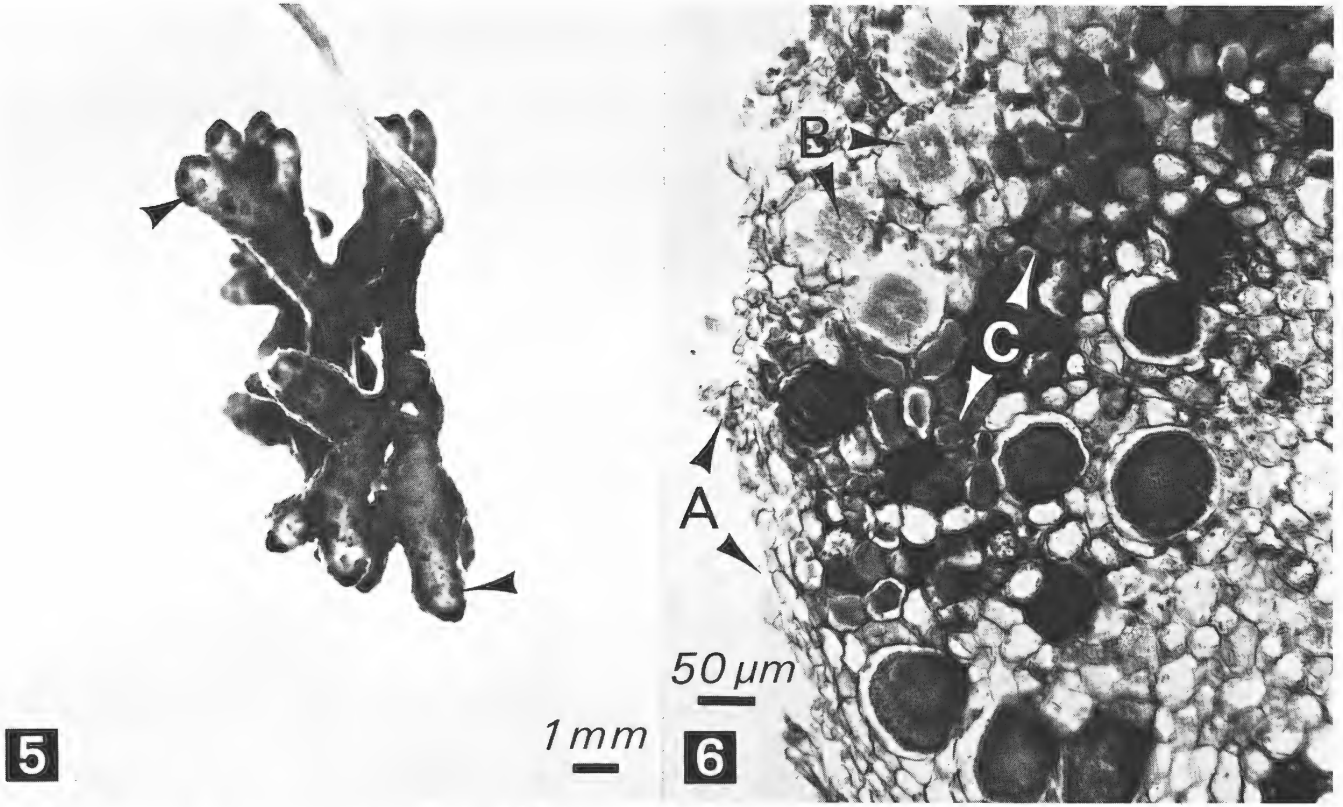

Figure 5. Young nodule with variously branched lobes. Dark blotches on lobe surface are sloughing patches of periderm (phellem). Figure 6. Transverse section near the proximal end of a nodule lobe. Note absence of periderm-like zone (A [compare to Fig. 3-A]); degenerating vesicle colonies (B); and zone of cortical cells filled with a dark-staining substance (C).

μm, septate) and (3 x 4 μm, club-shaped) (Hoeppel and Wollum 1971); in *Purshia tridentata* (0.33 0.55 μm) and 2.2-4.4 x 2.2-5.5 μm, spherical to obovoid) (Krebill and Muir 1974); and in *Cowania* (0.5 μm) and (2 x 3 μm, obovate to obpyriform). Some of these figures represent averages; others, ranges. *Cowania* endophyte vesicles were not strictly spherical, oval, or club-shaped, but in mycological terms (Snell and Dick 1971) they ranged from subglobose to obovate to obpyriform. It is not clear whether the variations reported are real endophyte differences or variation because of differing experimental observations and techniques.

Zones of endophyte development in nodule lobes were closely comparable to those described by van Dijk and Merkus (1976) and Becking (1977b) for *Alnus glutinosa* (L.) nodules. There were three distinct zones of development: (1) endophyte invasion of host cells, host cell and nuclear enlargement and expansion of the hyphal colony; (2) formation and presence of vesicles on the colony periphery with numerous amyloplasts in surrounding cells; and (3) degeneration of hyphal-vesicle colonies, and an associated disappearance of starch grains and a sloughing of host periderm and cortical cells.

Enlargement and hyperplasia of host nuclei in infected cells have been observed in *Ceanothus, Elaeagnus,* and *Myrica* nodule cells in earlier studies (Arzberger 1910, Furman 1959), but have not received recent interest. Association of the endophyte with the host nucleus during early invasion processes is seldom mentioned elsewhere. McLuckie (1923) noted endophyte "infection threads . . . coiling in the vicinity of the nucleus" in early invasion of young cortical cells of *Casuarina cunninghamiana* (Miq.). In their study of *Elaeagnus* and *Hippophae* nodules, Hawker and Fraymouth (1951) found what they termed an "endophyte plasmodium," first surrounding the host nucleus in early infection stages of cortical cells just behind the nodule apex. This close association may establish early control by the endophyte over the host nucleus, resulting in the modified host physiology expressed in nodule-endophyte development and function. The host nucleus remains visible in the endophyte-vesicle colony until the colony begins to decline. The host cell must also decline and die during this period. The numerous leucoplasts present in the vesicle zone gave a positive IKI stain and thus were suspected of being amyloplasts. Conspicuous hila present also indicated presence of starch grains. Unfortunately, normal roots were not examined for comparison, but the striking abundance of amyloplasts suggests an endophyte-induced accumulation of energy in the form of starch that is probably used primarily in endophyte-directed functions such as nitrogen fixation. *In vitro* reduction of C_2H_2 by vesicle clusters and other studies reviewed by Akkermans and Roelofsen (1980) indicate that vesicles are the site of nitrogen fixation.

Zones of periderm sloughing and exposure of degenerating cortical cells at the proximal end of nodule lobes could provide an avenue for release of endophyte spores or other propagules. Absence or failure to resolve other endophyte structures (such as sporangia, bacteroides, or granulated bodies) is perhaps not unusual. Young nodules were examined at the first branching stage. Possibly these structures form in older nodules, although sporangia formed in young *in vitro* cultures of the *Comptonia* endophyte (Newcomb *et al.* 1979).

Literature Cited

Akkermans, A. D. L., and W. Roelofsen. 1980. Symbiotic nitrogen fixation by actinomycetes in *Alnus*-type root nodules, pp. 279-299 *in*: W. D. P. Stewart and J. R. Gallon (edss.). Nitrogen Fixation A. Academic Press, London.

Arzberger, E. G. 1910. The fungous root-tubercles of *Ceanothus americanus, Elaeagnus argentea,* and *Myrica certifera,* pp. 60-101 *in*: Missouri Botanical Garden. 21st Annual Report.

Becking, J. H. 1970. Frankiaceae fam. nov. (Actinomycetales) with one new combination and six new species of the genus *Frankia* Brunchorst 1886, 174. Intern. J. Syst. Bacteriol. 20:201-220.

———. 1977a. Dinitrogen-fixing associations in higher plants other than legumes, pp. 185-275 *in*: Hardy, R. W. F., and S. W. Silver (eds.). A Treatise on Dinitrogen Fixation, Sect. III: Biology. John Wiley, New York.

———. 1977b. Endophyte and association establishment in non-leguminous nitrogen-fixing plants, pp. 551-567 *in*: Newton, W., J. R. Postgate, and C. Rodrigues-Barruecco (eds.). Recent Development in Nitrogen Fixation. 2nd International Symposium on Nitrogen Fixation, Salamanca, Spain. Academic Press, London.

Blauer, A. C., A. P. Plummer, E. D. McArthur, R. Stevens, and B. C. Giunta. 1975. Characteristics and hybridization of important intermountain shrubs. I. Rose Family. U.S. Department of Agriculture, Forest Service, Research Paper INT-169. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Bond, G. 1974. Root-nodule symbioses with actinomycete-like organisms, pp. 342-378 *in*: Quispel, A. (ed.). The Biology of Nitrogen Fixation. North Holland, Amsterdam.

———. 1976a. Observations on the root nodules of *Purshia tridentata.* Proc. R. Soc. Lond. B. 193: 127-135.

———. 1976b. The results of the IBP survey of root-nodule formation in non-leguminous angiosperms, pp. 443-475 *in*: Nutman, P. S. (ed.). Symbiotic Nitrogen Fixation in Plants. Cambridge Univ. Press. Cambridge, England. Interntl. Biol. Program, No. 7.

Furman, T. E. 1959. The structure of the root nodules of *Ceanothus sanguineus* and *Ceanothus velutinus,* with special reference to the endophyte. Amer. J. Bot. 46:698-703.

Hawker, L. E., and J. Fraymouth. 1951. A re-investigation of the root nodules of *Elaeagnus, Hippophae, Alnus,* and *Myrica,* with special reference to the morphology and life histories of the causative organisms. J. Gen. Microbiol. 5:369-386.

Hoeppel, R. E., and A. G. Wollum II. 1971. Histological studies of ectomycorrhizae and root nodules from *Cercocarpus montanus* and *Cercocarpus paucidentatus.* Can. J. Bot. 49:1315-1318.

Johansen, D. A. 1940. Plant Microtechnique. McGraw-Hill, New York and London.

Krebill, R. G., and J. M. Muir. 1974. Morphological characterization of *Frankia purshiae,* the endophyte in root nodules of bitterbrush. Northw. Sci. 48:266-268.

Lawrence, D. B., R. E. Schoenlike, A. Quispel, and G. Bond. 1967. The role of *Dryas drummondii* in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. J. Ecol. 55:793-813.

McLuckie, J. 1923. Studies in symbiosis. IV. The root nodules of *Casaurina cunninghamiana* and their physiological significance. Proc. Linnean Soc. New South Wales. 48:194-205.

Monsen, S. B. 1975. Selecting plants to rehabilitate disturbed areas, pp. 76-90 *in*: Campbell, R. S., and C. H. Herbel (eds.). Improved Range Plants. Soc. Range Manage., Denver, Colo.

Nelson, D. L. 1983. Occurrence and nature of actinorhizae on *Cowania stansburiana* and other Rosaceae, *in*: A. R. Tiedemann and K. L. Johnson (eds.). Proceedings—Research and Management of Bitterbrush and Cliffrose in Western North America (Symposium), 13-15 April 1982, Salt Lake City, Utah. Intermountain Forest and Range Experiment Station, USDA Forest Service.

Newcomb, W., D. Callaham, J. G. Torrey, and R. L. Peterson. 1979. Morphogenesis and fine structure of the actinomycetous endophyte of nitrogen-fixing root nodules of *Comptonia peregrina.* Bot. Gaz. 140(Suppl.):S22-S34.

Peterson, R. S., and R. G. Shurtleff, Jr. 1965. Mycelium of limb rust fungi. Amer. J. Bot. 52:519-525.

Plummer, A. P., D. R. Christensen, and S. B. Monsen. 1968. Restoring big-game range in Utah. Utah Div. Fish and Game, Publ. 68-3.

Righetti, T. L., and D. N. Munns. 1980. Nodulation and nitrogen fixation in cliffrose (*Cowania mexicana* var. *stansburiana* [Torr.] Jeps.). Plant Physiol. 65:411-412.

Sass, J. E. 1961. Botanical Microtechnique. Iowa State Univ. Press, Ames.

Snell, W. H., and E. A. Dick. 1971. A Glossary of Mycology. Harvard Univ. Press, Cambridge, Mass.

van Dijk, C., and E. Merkus. 1976. A microscopical study of the development of a spore-like stage in the life cycle of the root-nodule endophyte of *Alnus glutinosa* (L.) Gaertn. New Phytol. 77:73-91.

Received November 3, 1982
Accepted for publication February 17, 1983

Richard L. Everett

Intermountain Forest and Range
Experiment Station
University of Nevada
920 Valley Road
Reno, Nevada 89512

and

Kenneth Ward

Attorney at Law and Public Defender
Tonopah, Nevada 89409

Early Plant Succession on Pinyon-Juniper Controlled Burns

Abstract

Pinyon (*Pinus monophylla*)-juniper (*Juniperus osteosperma*) woodlands are too often burned to increase understory production without sufficient information on probable postfire response. Postburn vegetation response on six controlled pinyon-juniper burns in eastern Nevada demonstrated multiple entrance points into the standard successional model. Postfire succession was found to be partially explained by both initial and relay floristics successional theories. Species richness increased over time as species turnover rates declined and the proportion of perennial and preburn species increased. Several perennial forb species had maximum cover values during early succession. Predictability of early plant response to burning remains low because of the large species pool adapted to postburn conditions, inadequate detection of fire tolerant forb species, and unpredictable response from soil seed reserves. Once initial postburn plant response occurs, qualitative predictability of midsuccessional stages is thought to increase under the initial floristics successional model.

Introduction

Singleleaf pinyon (*Pinus monophylla* Torr. and Freem)-Utah juniper (*Juniperus osteosperma* (Torr.) Little) woodlands of the Great Basin are increasing in area and density with a concomitant loss of forage for livestock and wildlife (West *et al.* 1975). This widespread phenomenon in the western pygmy forests is generally thought to be largely the result of fire suppression and concurrent livestock grazing (Barney and Frischknecht 1974, Burkhardt and Tisdale 1969). A management response to restore the "natural state" has been controlled burning of woodland stands.

In the past, the standard postfire pinyon-juniper successional model presented succession as an ordered series of life forms from the annual forb to the tree stage (Erdman 1970, Barney and Frischknecht 1974). These models were useful in describing the general trends in succession. Recent reemphasis that succession is a species-by-species process (Drury and Nisbet 1973, Werner 1976) dependent upon a species "vital attributes" (Noble 1981) and the resurgence of Gleason's (1917) individualistic community theory in the form of "multiple successional pathway concepts" (Cattelino *et al.* 1979) has prompted a reevaluation of these standard models. If, as Noble (1981) suggests, there is no "unifying successional scheme" but only a collection of species specific trends (Pickett 1976), then a rigid adherence to the standard successional model could be disadvantageous to land managers making fire response predictions.

The dominant successional pathway may enhance or constrain the predictability of

postburn response. Succession may proceed by "relay floristics," the sequential migration to and dominance of the site by later successional species, or by "initial floristics," the sequential dominance of the site by higher successional species present on the site immediately following disturbance, or by both (Egler 1954). Early successional species may modify the site to the benefit of later-occurring species (facilitation model), or later successional species may just tolerate long periods of supression (tolerance model) (Connell and Slatyer 1977). Predictability of response increases relative to the response potential for remnant plants and inversely with an increase in the size of the species pool that can immigrate to the site or emerge from undefined soil and seed reserves. Thus, initial floristic-tolerance model controlled systems should be more predictable in succession pattern than relay floristic-facilitation model controlled systems influenced by chance migration factors.

This paper examines plant response on six prescribed burns in the pinyon-juniper woodlands, tests results against a standard pinyon-juniper successional model (Erdman 1970), and examines the relative importance of relay and initial floristics in succession Cover of major species is also examined to relate individual species response to the successional process.

Study Site

Controlled burns were conducted in 1975 and 1976 on alluvial terraces and drainage bottoms at an elevation of approximately 2000 m in a pinyon-juniper woodland on the east slope of the White River Mountains in eastern Nevada. Sites selected for burning appeared similar in cover of major plant species. Ellenberg's cover similarity index (Mueller-Dombois and Ellenberg 1974, p. 215) gave high similarity index values among sites, corroborating this observation. Soils of the burns are similar, having been previously described by Ward (1977) as Aridic Argixerolls. Livestock grazing was intensive in the late 1800s and early 1900s, but since the 1960s sites have been used only as summer range under moderate stocking rates. No livestock use occurred on any site after burning.

The climate is semiarid, with a mean annual precipitation of 225 mm fairly evenly distributed, peak winter snows in December, and peak summer thunderstorms in June (20 years of record, Lund, Nevada, elevation 1700 m, 41 km east of study area). On-site precipitation from 1 April to 15 September, as determined by a standard rain can, was 86 mm (1976), 203 mm (1977), and 76 mm (1978).

Methods

Six controlled burns were conducted at various times in the spring, summer, and fall. Method of burning and concurrent environmental conditions have been previously described by Bruner and Klebenow (1979). Smudge pot lighters (filled with 50 percent gasoline and 50 percent diesel oil were used to burn scattered and dense stands of pinyon-juniper under conditions of low relative humidity (8-26%) and soil moisture (2-13%), moderate air temperatures (12-25°C), wind speeds (13-42 kph), and vegetative cover (42-56%) (Bruner and Klebenow 1979). Burning intensity varied among burns, but all burns were sufficiently intense to consume most aboveground understory vegetation less than 0.3 mm in diameter. On three sampled burns, the maximum surface soil temperatures in the interspace between trees were 305°, 200°, and 310°C; soil

surface temperatures under bitterbrush (*Purshia tridentata* (Pursh.) D. C.) plants exceeded that of the interspace by 200° to 400° (Klebenow *et al.* 1977).

Vegetative cover of understory species was recorded prior to burning and at the end of the growing season following the burn for 4 to 5 years. Detailed description of the sampling methods has been previously reported (Ward 1977). Briefly, at each potential burn site a set of two or three permanent transects, 30 m in length, were established. The line-intercept technique (Canfield 1941) was used to estimate tree and shrub cover. Grass and forb cover was estimated using Daubenmire's (1959) canopy coverage method within 15 microplots (30 × 60 cm) established at every other meter mark along the transect. Species nomenclature used followed that of Holmgren and Reveal (1966).

Preburn and postburn cover data from the transects were summed by species and plant form (annual forb, perennial forb, perennial grass, and shrub) and means derived for each burn. Annual grasses were rare on the sites and not considered further. The proportion of the preceding year's species pool lost from one year to the next (species turnover rate), percent of original preburn species present, species richness, and plant cover were used to characterize the pre- and post fire plant assemblages. Paired "t" tests of differences between means were used to evaluate selected phenomena at the 5 percent probability level following tests for skewness and kurtosis (Snedecor 1956).

Results and Discussion

Successional Pathways

Plant succession following fire has previously been presented as a series of contiguous stages with one plant form following the other (Fig. 1, Erdman (1970)). Our data suggests that succession is site specific and starts from a continuum of preburn assemblages such that there are multiple entrance points into the successional model (Fig 1B).

Annual forbs coyote tobacco (*Nicotiana attenuata* Torr.), flixweed tansymustard (*Descurainia sophia* (L.) Webb), and goosefoot (*Chenopodium album* L. var. *album*) dominated response on the 25 April burn, but this was the only burn that closely followed the successional models of either Erdman (1970) or Barney and Frischknecht (1974) (Fig. 2.) Rapid regrowth of perennials, the shrub Douglas rabbitbrush (*Chrysothamnus viscidiflorus* (Hood) Nutt. var. *viscidiflorus*), and perennial forbs tailcup lupine (*Lupinus caudatus* Kellog) and skullcap (*Scutellaria nana* A. Gray), altered the standard successional pathway in postburn vegetation of 9 May, 9 October, and 22 June burns, respectively; but regrowth was insufficient to prevent subsequent dominance or codominance by annual forbs tumblemustard (*Sisymbrium altissimum* L.), eriastrum (*Eriastrum sparsiflorum* (Eastw.) Mason), groundsmoke (*Gayophytum ramosissimum* Nutt.), stickseed (*Lappula redowskii* (Hornem.) Green), and goosefoot (Fig. 2). Germinating soil seed reserves of the perennial forb Munro globemallow (*Sphaeralcea munroana* Dougl.) provided sufficient plants to dominate the postburn vegetation on the 13 June burn, and regrowth of Douglas rabbitbrush was sufficient to almost continuously dominate plant response on the 3 May burn (Fig. 2).

Differences in plant form dominance among the six burns indicate succession starts from multiple points along the successional model (Fig. 1B). The data suggests that, given a sufficient number of burns, we would find a continuum of plant form combinations in early postfire plant assemblages.

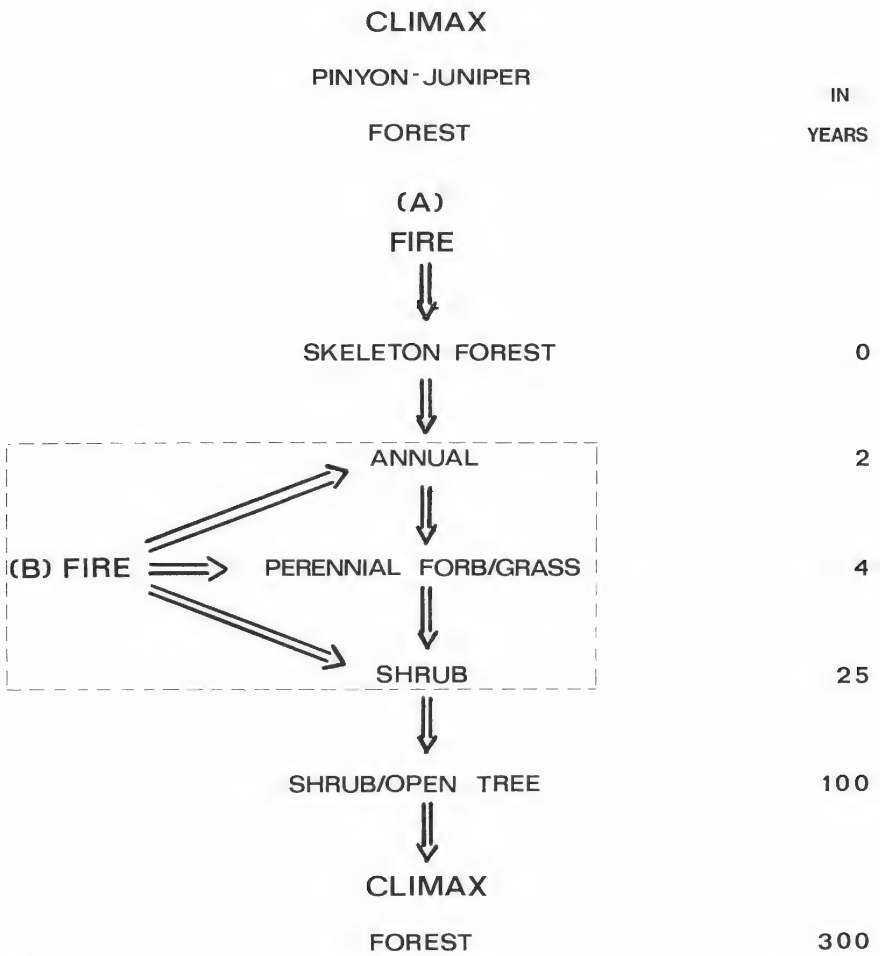

Figure 1. Successional model of pinyon-juniper woodland following fire (Erdman 1970). Multiple entrance points into the successional model. (A & B)

The ebb and flow of species were not consistent among the burns so there was no single scenario of species changes during early succession. On the 25 April burn first coyote tobacco then flixweed tansymustard and then stickseed predominated on the site. On the 9 May burn groundsmoke and goosefoot gave way to stickseed, but eriastrum was continually the dominant annual forb on the 9 October burn.

The annual forb stage may be skipped if succession has already eliminated annuals from the stand and fire responsive perennial species can rapidly reoccupy the burn. The presence and magnitude of the annual forb stage was dependent upon the creation of a regenerative niche (Noble 1981) due to the absence of perennial species regrowth or establishment from soil seed reserves. There was a "gradient of decreasing opportunities" (Pickett 1976) for annual forb dominance as the initial response of perennial forbs and shrubs increased. On the 3 May, 12 June, and 22 June burns a definite annual

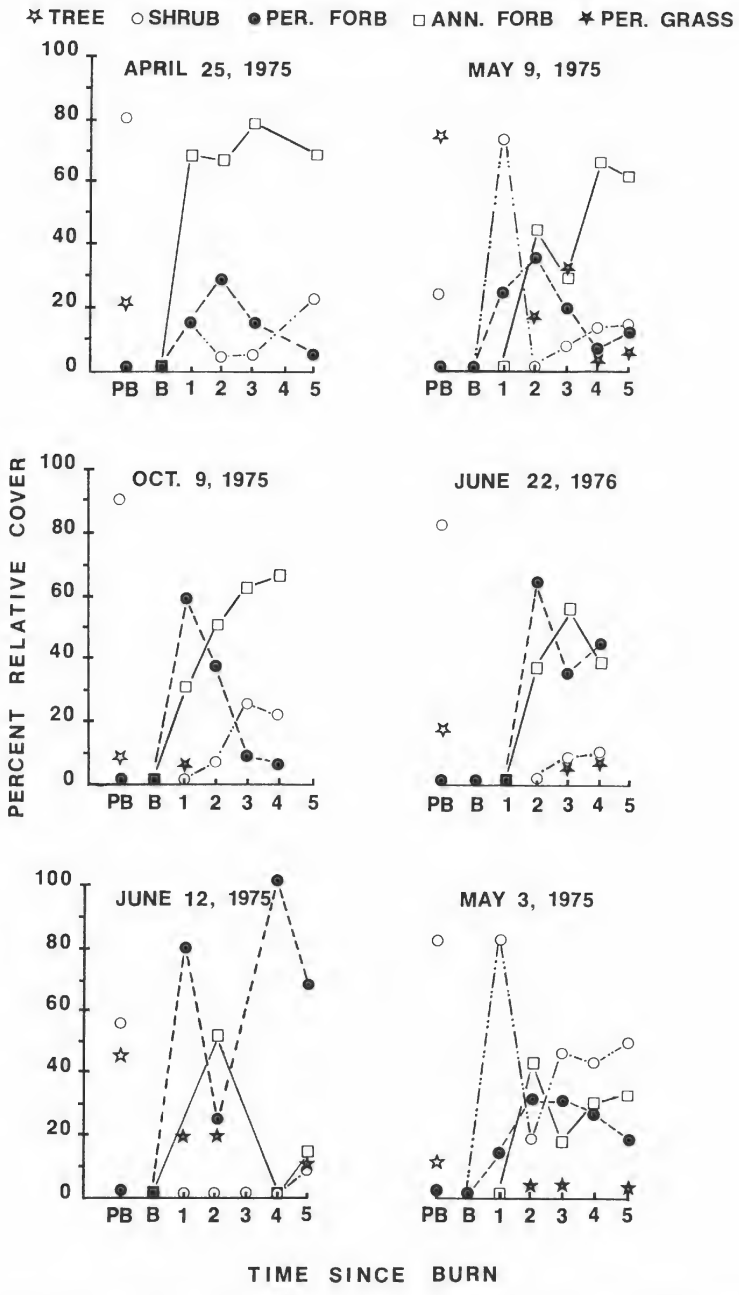

Figure 2. Percent relative cover by plant form on the six burns by number of growing seasons since burn occurred. (PD = preburn; B = burn date; 1-5 = postburn growing seasons.)

forb stage did not occur (Fig. 2), but instead skullcap, Munro globemallow, and Douglas rabbitbrush dominated the respective sites. The skipping of early successional stages (Fig. 1B) was previously suggested by Barney and Frischknecht (1974).

Successional Processes and Predicting Plant Response

The rapid return of preburn species to the burn sites and the appearance of species dominant in midsuccession (shrubs) seems to predispose the character of later successional stages. All burns had several plant forms (shrub, forb, grass) present almost immediately following fire, including many present in the preburn vegetation (Fig. 2). The data, therefore, indicate "initial floristics" (Egler 1954) or "tolerance" (Connell and Slatyer 1977) successional models are appropriate for early to midsuccessional stages. Succession proceeding on an "initial floristics" basis denotes an internally controlled system, a system with a measure of qualitative predictability (Lyon and Stickney 1976).

Preburn prediction of early plant response can be negated when fire-tolerant forbs are not obvious in preburn vegetation and/or plant response comes from soil seed reserves. Numerous forb species recorded on burn sites were apparently absent in preburn vegetation. Munro globemallow had moderate postburn cover values (14 percent, 12 June burn and 4 percent, 3 May burn) but was not recorded in preburn vegetation on either site. Plummer *et al.* (1957) reported dramatic increases in *Sphaeralcea* spp. following tree harvesting of pinyon (*Pinus edulis* Engelm.) and Utah juniper and ascribed *Sphaeralcea* spp. response to germination of soil seed reserves. Stimulation of Munro globemallow seed reserves following a fire could be expected as both alternating temperature extremes and increased nitrate levels (characteristics of burned soils) have been shown to increase *Sphaeralcea* spp. germination (Page *et al.* 1966).

Postburn succession was not observed through the tree stage. But the absence of singleleaf pinyon in early succession, its low seed viability, and its requirement for a nurse plant (Phillips 1909) indicate relay floristics (Egler 1954) must determine the rate of pinyon tree reinvasion and thus the character of later successional stages. Pinyon establishmen from postburn seed caches by birds (Vander Wall and Balda 1977, Ligon 1978, Lanner and Vander Wall 1980) or rodents (our observation) are probably the principal migration processes.

Plant Assemblage Response

A relatively large species pool was adapted to postburn conditions, including many preburn species. Postburn plant assemblages contained numerous new perennial (12) and annual (14) forbs. No new shrub species and only two grass species occurred after the burns.

Species richness of both perennial and annual species increased over preburn conditions, especially the annuals (Fig. 3). This figure graphically demonstrates Pickett's (1976) "gradient of decreasing opportunity" for annual species establishment as perennial species numbers and dominance (preburn) increased. The data corroborates Nabi's (1978) report of decreasing species richness during pinyon-juniper succession.

The proportion of preburn species in postfire plant assemblages increased rapidly (>60 percent) lending credence to the use of Egler's (1954) initial floristics model on these sites (Fig. 4). The species turnover rate (proportion of species lost from the preceding year's species pool) declined over the same period (Fig. 4). The return

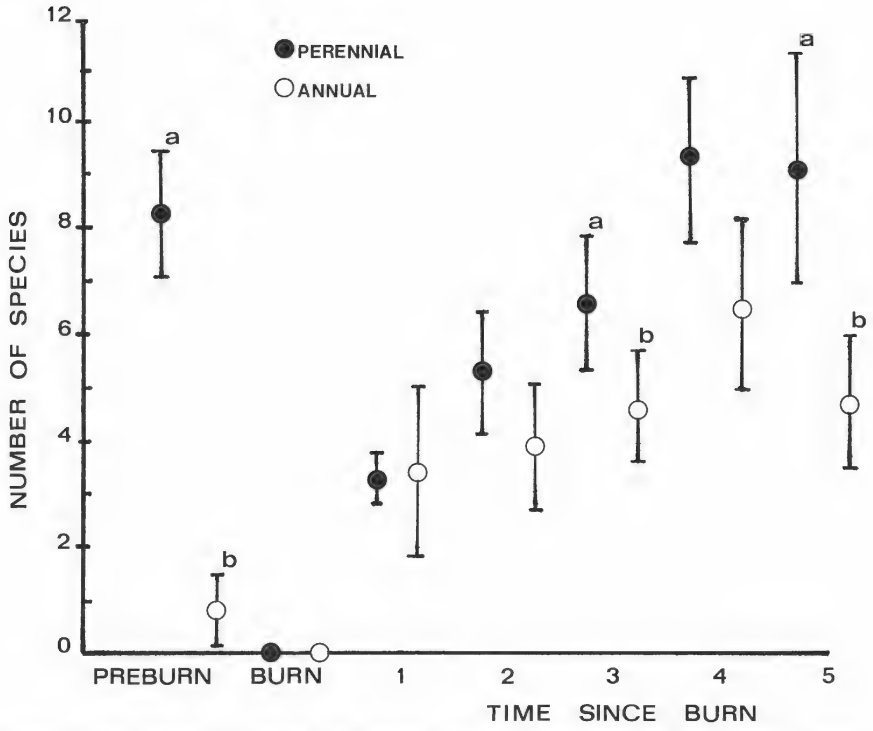

Figure 3. Mean number of perennial and annual species on the six burn sites by number of growing seasons following burning. Vertical bars reflect two standard errors of the mean and denote the range in expected mean response from a sample of six burns. Significant differences ($p = 0.05$) between annual and perennial species are denoted by superscripts and were determined from "t" test of differences on each site.

of preburn species did not precipitate this decline in species turnover; rather the number of species lost each year remained fairly constant as the total number of species and the proportion of perennials increased. Reinvading preburn species had significantly ($p = 0.05$) less cover ($\bar{\chi} = 7.1\%$) than new postfire species ($\bar{\chi} = 19.8\%$) for four to five growing seasons following burning. The decline in species turnover was interpreted as indicating the remaining species were more adapted to conditions in the developing plant assemblage than their more opportunistic predecessors.

The mean plant cover on burn sites rapidly returned to two-thirds of the original cover (Fig. 5), but this is a group mean and individual burn sites differ. Cover provided by annual species was so variable among years that total cover for a burn could decrease as well as increase over time. Vertical bars in Fig. 5 reflect two standard deviations from the mean and show the wide range in cover among sites. Preburn conditions indicate cover should increase as shrub and tree species become dominant.

Individual Species Response

Noble (1981) suggests a working knowledge of species' "vital attributes" during regeneration, establishment, and reproductive phases is required to accurately predict succes-

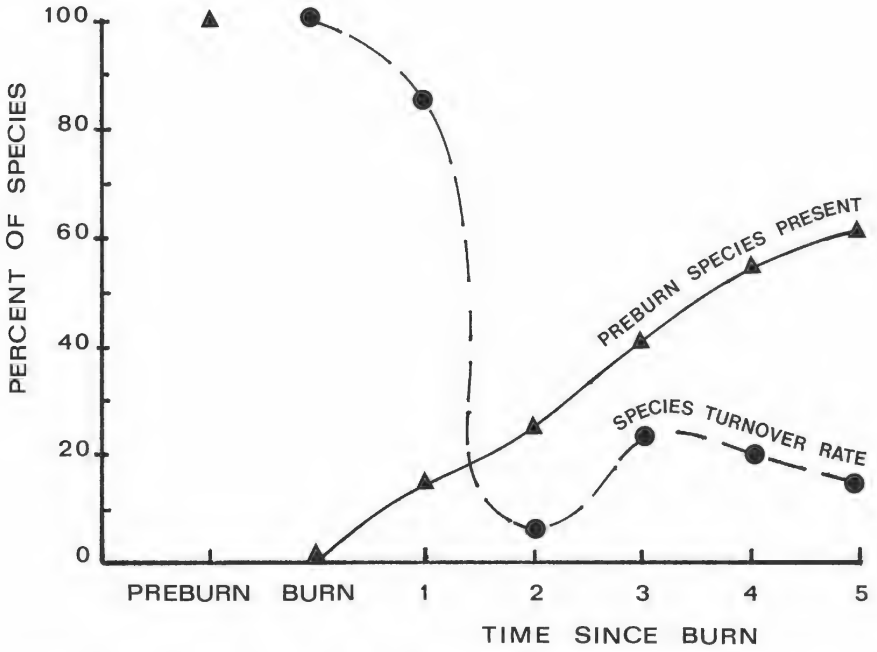

Figure 4. Percent species turnover rate and percent of preburn species present on the six burns by number of growing seasons following burning. (Turnover rate = proportion of total species lost from one year to the next.)

sion. At the time of this study there was little information available on the fire response of the observed species, and often the presence of indivdual species on burns was not predictable. Now we can provide information on the rapid increase and decline of major understory species and, in part, explain observed changes in plant form and species composition over time. This information is rudimentary and provides only a base for further individual species investigation.

As anticipated by earlier successional models, several annaul forb species exhibited a short cycle to maximum cover on these burns. Two examples are Groundsmoke and Coyote tobacco, which had vigorous growth on a given site for only one growing season (Fig. 6A). Coyote tobacco cover peaked the second growing season following seed dispersal from scattered but extremely robust plants that occurred the previous year. Groundsmoke cover peaked four growing seasons after fire, and Stickseed (not shown) had yet to reach maximum cover at the conclusion of this study. Time and height of cover peaks in Fig. 6A represent successional phenomena and are not solely the result of climatic factors. All burns were not conducted in the same year, and not all species responded favorably to the wettest year, 1977. The first growing season following the 25 April and 3 May burns was in 1976, but for the 9 October and 22 June burns, the first growing season was in 1977.

Coyote tobacco, groundsmoke, and several other annuals had only a short period of vigorous growth in which to replenish soil seed reserves. If site conditions during the

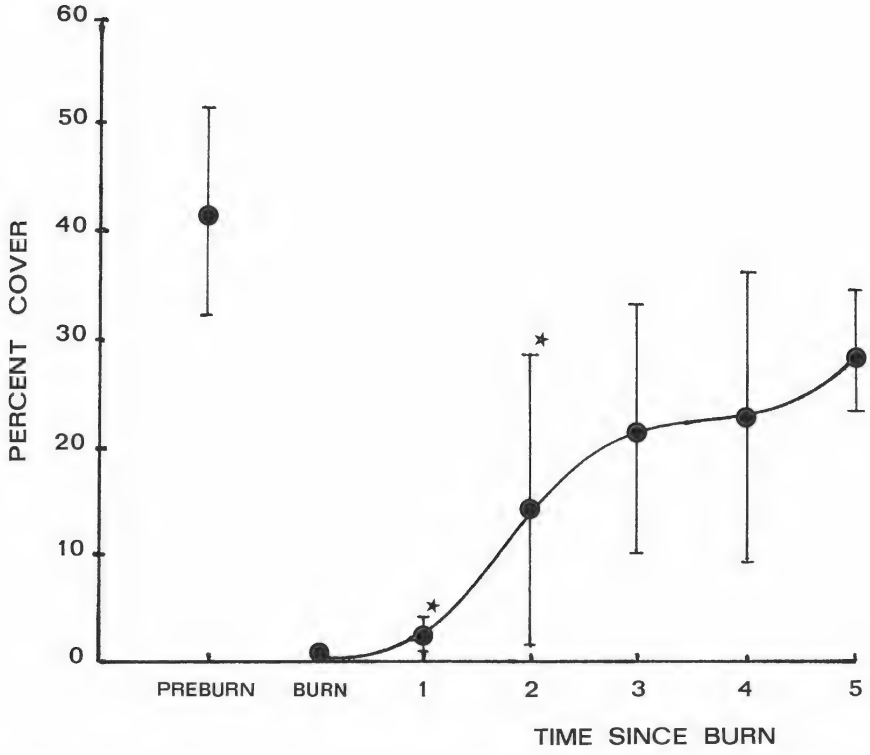

Figure 5. Mean percent herbaceous cover on the six burns by growing season following burning. Vertical bars reflect two standard deviations from the mean. The symbol * denotes significant ($p = 0.05$) difference in cover from the previous year.

last catastrophic event prohibited this annual forb expression, then the lack of annual forb response following some of the current burns appears convincing.

Several of the perennial forbs also show rapid peaks in cover. Relatively high cover values occurred only for a short time (2-3 years) and in early succession for prickly poppy (*Argemone polyanthemos* (Fredde) G. B. Owenby), skullcap, tailcup lupine, and Munro globemallow (Fig. 6B). Peaks in cover generally occurred the third or fourth growing season following fire and lasted for two growing seasons. These perennial forbs had a limited period of maximum growth and reproduction potential that occurred in early succession, although they may remain secondary components of the plant assemblage for long periods of time.

Penennial grass cover was noticeably lacking in postburn vegetation. Preburn cover values were low, and postburn remnant plants could not respond sufficiently to make a significant contribution to postburn plant cover. Postburn response by isolated plants of Breat Basin wildrye (*Elymus cinereus* Scribn. and Merr.) was dramatic, but the species did not occur in great numbers on a majority of the burn sites.

Douglas rabbitbrush increased from a preburn cover of 3 to 14 percent on the 3 May burn by rapidly resprouting from burned crowns. Harniss and Murray (1973) reported

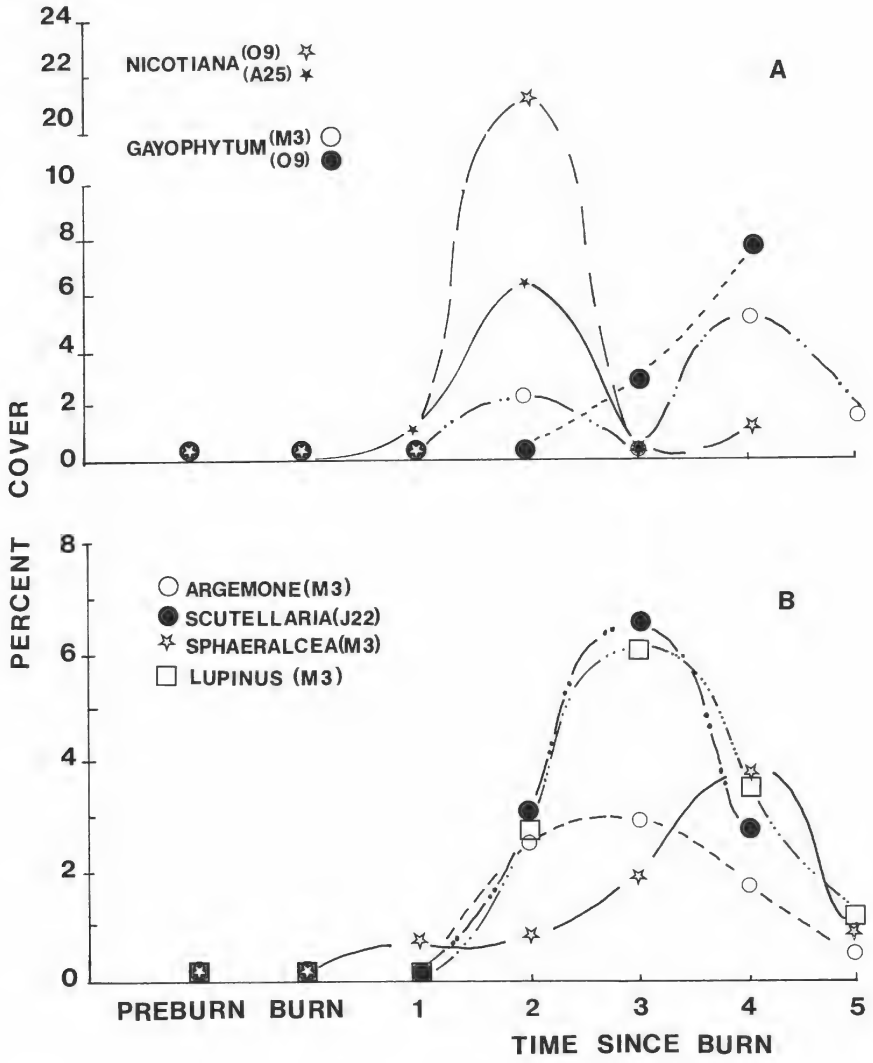

Figure 6. Cover of *Nicotiana attenuata* and *Gayophytum ramosissimum* by number of growing seasons since burning. (A & B) Cover of *Argemone polyanthemos*, *Scutellaria nana*, and *Sphaeralcea munroana* and *Lupinus* spp. by growing season following burning. Data for burns on 24 April (A25), 3 May (M3), 22 June (J22), and 9 October (O9) are presented.

a sharp increase in rabbitbrush cover following burning and a decline in cover after 10 years. Douglas rabbitbrush must decline on these sites if the species is to return to preburn cover levels. Desert bitterbrush (*Purshia glandulosa* Curran) cover declined after burning but is increasing slowly. Postfire Desert bitterbrush cover was derived solely from postburn rodent cache seedlings (Ward 1977).

Conclusions

Early plant succession on pinyon-juniper burns in the study area suggests multiple entrance points into the standard successional model. Variability in the entrance point is the rule rather than the exception, as seen in the variation in plant response observed among burns conducted at approximately the same time in a given year. If a burn is large enough, we could expect several early successional stages to occur concurrently.

Prior to burning, quantitative predictability of immediate postburn vegetation is difficult because of unobtrusive fire-tolerant herbaceous species, unpredictable response from soil seed reserves, variable postfire weather, and a large species pool of plants adapted to postburn conditions. The consistent postfire growth response from root sprouting shrubs, bunchgrass (Great Basin wildrye), and a few perennial forbs allow us to make qualitative estimates, but no more. Where remnant plant survival is more robust or the potential postburn species pool reduced, response may be more predictable because opportunism is depressed. Knowledge of species "vital attributes" (Noble 1981) may improve our predictability of plant response in the future, but a fundamental problem remains in predicting what species will be present in the postburn plant assemblage and whether postfire conditions will be favorable for the species to exhibit these "vital attributes." Once initial postburn plant response occurs, qualitative predictability of midsuccessional stages increases under the initial floristics successional model.

Initial and relay floristics successional models are both operative in pinyon-juniper succession. Original preburn species rapidly reappear on the burns, perennial species outnumber annuals, and the species turnover rate rapidly declines (initial floristics); but relay floristics (migration) determines the character of later stages, as we did not find singleleaf pinyon seedlings.

Understory cover increased rapidly to two-thirds of the original preburn total for sites taken collectively. The composition of this cover changed as numerous species were gained and lost from the plant assemblage. Many perennial and annual forb species had only a short period of maximum growth during early succession. Thus, if species expression is inhibited by climate or competition, alternate successional pathways are thought to occur following the next burn period.

Acknowledgments

Dr. Wilbert Blackburn, Dr. Donald Klebenow, and Mr. Allen D. Bruner (University of Nevada Agricultural Experiment Station) were instrumental in establishing this study and acquiring the initial data base. Mr. Garth Baxter, Mr. Paul Demule, Mr. Wayne Sevenson, and Mr. Mike Lawrence of the USDA Forest Service White Pine Ranger District contributed much to the success of the project and provided pertinent information on past grazing use. Mr. Clay Gautier, Mr. Kenneth Small, and Ms. Susan Koniak collected field data and contributed to the study.

Literature Cited

Barney, M. A., and N. C. Frischknecht. 1974. Vegetation changes following fire in the pinyon-juniper type of west-central Utah. J. Range Manage. 27: 91-96.

Bruner, A. D., and D. A. Klebenow. 1979. Predicting Success of Prescribed Fires in Pinyon-Juniper Woodland in Nevada. USDA For. Serv. Res. Pap. INT-219.

Burkhardt, J.W., and E. W. Tisdale. 1969. Nature and successional status of western juniper vegetation in Idaho. J. Range Manag. 22: 264-270.

Canfield, R. H. 1941. Measurement of grazing use by the line interception method. J. For. 42: 192-194.

Cattelino, P. J., I. R. Noble, R. O. Slatyer, and S. R. Kessel. 1979. Predicting the multiple pathways of plant succession. Environ. Manage. 3: 41-50.
Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Natur. 111: 1119-1144.
Daubenmire, R. 1959. Canopy coverage method of vegetation analysis. North. Sci. 33: 43-64.
Drury, W. H., and I. C. Nisbet. 1973. Succession. J. Arnold Arboretum 54: 331-368.
Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition a factor in old-field vegetation development. Vegetato 4: 412-417.
Erdman, J. A. 1970. Pinyon-Juniper Succession after Natural Fires in Residual Soils of Mesa Verde, Colorado. Brigham Young Univ. Sci. Bull. Bio. Series 11(2).
Gleason, H. A. 1917. The structure and development of the plant association. Bull Torrey Bot. Club 43: 463-481.
Grubb, P. J. 1977. The maintenance of species richness in plan communities: the importance of regeneration niche. Biol. Rev. 52: 107-145.
Harniss, R. O., and R. B. Murray. 1973. Thirty years of vegetal changes following burning of sagebrush-grass range. J. Range Manage. 26: 322-325.
Holmgren, A. H., and J. L. Reveal. 1966. Checklist of the vascular plants of the intermountain region. USDA For. Serv. Res. Pap. INT-32.
Klebenow, D., R. Beall, A. Bruner, R. Mason, B. Roundy, W. Stager, and K. Ward. 1977. Controlled fire as a management tool in the pinyon-juniper woodland, Nevada. Summary Progress Report, Univ. Nevada Agric. Exp. Sta. Mimeograph.
Lanner, R. M. and S. B. Vander Wall. 1980. Disposal of limber pine seed by Clark's Nutcracker. J. For. 78(10): 637-639.
Ligon, T. D. 1978. Reproductive interdependence of Pinyon Jays and pinyon pines. Ecol. Monogr. 48: 111-126.
Lyon, L. J., and P. F. Stickney. 1976. Early vegetal succession following large northern Rocky Mountain wildfires, pp. 355-375 *in*: Proc. Montana Tall Timbers Fire Ecology Conference and Fire and Land Management Symposium, No. 14, 1974, Tall Timbers Research Station, Tallahassee, Florida.
Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.
Nabi, A. A. 1978. Variation in Successional Status of Pinyon-Juniper Woodlands in the Great Basin. M.S. thesis, Utah State Univ., Logan.
Noble, I. R. 1981. Predicting successional change, pp. 278-301 *in*: Fire regimes and ecosystem properties. Proc. of the conference, Dec. 11-15 1978, Honolulu, Hawaii. USDA For. Serv. Gen. Tech. Rept.
Page, R. J., D. L. Goodwin, and N. E. West. 1966. Germination requirements of scarlet globemallow. J. Range Manage. 9: 145-146.
Phillips, F. J. 1909. A study of pinyon pine. Bot. Gaz. 43: 216-223.
Plummer, A. P., P. L. Jensen, and H. P. Stapely. 1957. Game Forage Revegetation Project. Utah Div. of Wildlife Res. W-82-R-3.
Pickett, S. T. A. 1976. Succession: an evolutionary interpretation. Am. Nat. 110: 107-119.
Snedecor, E. W. 1956. Statistical Methods Applied to Experiments in Agriculture and Biology. Iowa State Univ. Press, Ames, Iowa.
Vander Wall, S. B., and R. P. Balda. 1977. Coadaptations of the Clark's nutcracker and pinyon pine for efficient seed harvest and disposal. Ecol. Monogr. 47: 89-111.
Ward, K. O. 1977. Two-Year Vegetation Response and Successional Trends for Spring Burns in the Pinyon-Juniper Woodlands. M.S. Thesis, Univ. Nevada, Reno.
Werner, P. A. 1976. Ecology of plant populations in successional environments. Systematic Bot. 1: 246-268.
West, N. E., K. H. Rea, and R. J. Tausch. 1975. Basic synecological relationships in juniper-pinyon woodlands, pp. 11-53 *in*: G. F. Gifford and F. E. Busby (eds.) The Pinyon-Juniper Ecosystem. Utah Agr. Exp. Stn.

Received January 26, 1982
Accepted for publication March 8, 1983

Keith B. Aubry

College of Forest Resources, AR-10
University of Washington
Seattle, Washington 98195

The Recent History and Present Distribution of the Red Fox in Washington

Abstract

In Washington, indigenous red foxes *(Vulpes vulpes cascadensis)* occur in habitats at high elevations in the Cascade Mountains. Introduced red foxes have long occupied the lowlands of western Washington, yet neither their distribution nor the circumstances of their introduction has been documented. Non-native red foxes were intentionally introduced into several areas of western Washington; fox farms, both east and west of the Cascades, also contributed to the introductions. Distribution records of red foxes were collected from State and Federal agencies, museums, and correspondence with trappers from Washington. Three introduced populations of red foxes inhabit Washington State: a widely distributed population west of the Cascades and two less extensive populations east of the Cascades. Red foxes do not occupy the Blue Mountains of southeastern Washington, as was generally assumed, and red foxes in northeastern Washington are descended from introduced animals and do not belong to the Rocky Mountain or Cascade subspecies. The range of the Cascade red fox in Washington is similar to previous reports, but more restricted in extent, since some records from low elevations had been incorrectly assigned to the indigenous population.

Introduction

In the State of Washington, fur-trapping is a widespread recreational and economic activity. One hundred or more red foxes *(Vulpes vulpes)*, may be harvested annually, the great majority of which are from areas at low elevations in the western portion of the State (Wash. State Dept. Game, 1976-1980). Standard works, which present detailed distributional information for red foxes in Washington (Dalquest 1948, Ingles 1965, Hall 1981), refer only to the indigenous Cascade red fox *(V. v. cascadensis)*. This variety is reportedly restricted to mountainous regions. No consideration was given to populations occurring at low elevations. The presence of an introduced 'lowland' red fox in the Puget Sound region, however, has long been recognized by residents and by personnel of the Washington State Department of Game. A comprehensive evaluation of the distribution of red foxes in Washington is needed, given the importance of introduced red foxes as furbearers and the possibility of their competing and interbreeding with native Cascade foxes.

In the western United States, indigenous populations of the red fox occupy subalpine meadow and parkland habitats. The Cascade red fox is found in the Cascade Mountains of Oregon, Washington, and southern British Columbia; the Sierra Nevada red fox *(V. v. necator)*, in the Sierra Nevada Range of California; and the Rocky Mountain red fox *(V. v. macroura)* in the Rocky Mountains from New Mexico to Montana and the southern Canadian Rockies, and west to Idaho and the Blue Mountains of Oregon (Bailey 1936a). During the early 1900s, when western areas of the continent were being settled, populations of red foxes became established in valleys at low elevations and along coastal areas. In Oregon, red foxes are also found near the northwestern coast (Bailey 1936b, Maser *et al.* 1981) and in the Willamette Valley, west of the Cascades (Livezey

and Evenden 1943, Maser *et al.* 1981). According to Ingles (1965), these lowland populations are the result of introductions from the southern United States. Grinnell *et al.* (1937) reported that the population of red foxes in the Sacramento Valley of northern California is geographically isolated from the population in the Sierra Nevada and that red foxes were probably introduced sometime prior to 1900, although the circumstances of the introduction could not be determined. Recent work (Gray 1977) indicates that the Sacramento Valley population has significantly expanded its range since that time. In a review of the distribution of red foxes in Idaho, Fichter and Williams (1967) documented their presence in habitats previously unoccupied by the species, such as cultivated areas, cool deserts of the foothills, and the Snake River Plain. This range expansion is largely attributed to downslope movement by Rocky Mountain foxes, but they do not exclude the possibility that these populations result from accidental introductions. Fox farms were present in southern Idaho in the early part of the century, and the authors described several instances of individuals escaping from such farms.

Available information on the lowland red fox in Washington is limited and appears to have been based on documented records. Lauckhart (1970) claims that two races of red fox are present: a rare, indigenous high mountain form and a common, introduced lowland form whose ranges are separated by uninhabited expanses of forested foothills and mountains. Larrison (1970) assigns the lowland red fox to the subspecies *fulva* of the eastern United States and claims that it had been introduced into the Kitsap Peninsula in Puget Sound, farmlands south of the Olympic Peninsula, and the northeastern Puget Sound region. This form of red fox is now reported from nearly all lowland areas of western Washington. Lauckhart (1972) asserts that the Eastern red fox began to appear in the Skagit Valley of the north-eastern Puget Sound region sometime in the 1920s. The source of this population is believed to have been red foxes brought into the area by hound hunters, but he further speculates that escaped animals from private fur farms might have accelerated the spread of this population.

Methods and Materials

During three winter trapping seasons (1978 to 1980), all registered trappers in Washington were contacted by mail. They were asked to provide detailed reports of all previous sightings or trappings of red foxes and to include any information regarding the introduction of red foxes into Washington. Over the three year period, an average of about 1900 trappers from all areas of the State were contacted each year. I received 153, 38, and 74 replies for the years 1978, 1979, and 1980, respectively. Local trappers are probably better informed about red foxes in Washington than any other sizeable group of people. Trappers are distributed throughout the state, and some have lived and trapped in this region for most of the century. I therefore believe that they can accurately identify red foxes and are a reliable source of information on the history of red foxes in Washington.

Records of the Washington State Dept. of Game, National Park Service, and U.S. Forest Service were searched for pertinent information. All museums in the United States and Canada that potentially contained red fox material from Washington (Choate and Genoways 1975) were either visited or contacted by mail to obtain locality records of specimens.

All records that could be located on a map to an area less than one township in ex-

tent were used. These were plotted on a 1:500,000 scale USGS map of Washington. Areal, elevational, and ecological information were used to delineate boundaries around populations of red foxes. West of the Cascade Crest, red foxes occur either in relatively undisturbed habitats in mountainous regions, or at lower elevations in areas of human settlement. A wide, uninhabited zone of dense forest separates fox populations in these two areas, and boundaries around each were easily drawn. Because forested habitats differ east of the Crest, no such 'buffer zone' exists there. Nevertheless, eastern records are also either from relatively unsettled, forested areas at high elevations or from non-forested areas at lower elevations near towns or along river valleys and highways. Therefore, east of the Cascade Crest, records are assigned to introduced populations if a source of introduction in the area is documented and the records are from areas of human activity at low elevations. Records are assigned to the Cascade population if they are from the less disturbed forested habitats at higher elevations.

Results and Discussion

History of Introductions

Introductions of red foxes, both intentional and accidental, are shown in Fig. 1. Mr.

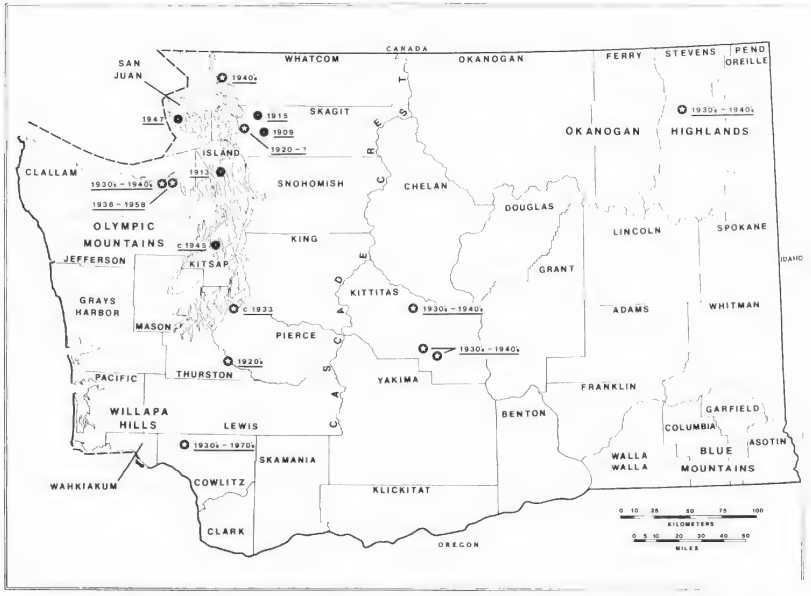

Figure 1. Dates and locations of fox farms (circled stars) and points of introduction of red foxes (solid circles) in Washington.

Floyd G. Squires, a long-term resident of Bow, Washington, in western Skagit Co., has spoken to many 'old timers' in the area, and informed me that in "1909, two females and one male were imported from the State of Illinois . . . each vixen produced a litter of pups which were raised and released that fall. Shortly after the release of the pups, both females escaped from the enclosure. The male was released the following day." The next spring, one of the females was observed denning on a nearby ridge. Accord-

ing to the 'old timers,' red foxes did not occur in Skagit Co. at that time and were introduced for hunting with hounds by settlers who came from the southeastern United States and missed having red foxes to hunt. He further stated that "about 1915, . . . between five and eight fox were released on the south side of Alger Mountain [in northwestern Skagit Co.]. These fox . . . were also from the State of Illinois." This last report was confirmed by M. Splane of Sedro Wooley, Skagit Co., who was interviewed by Scheffer (1939) and reportedly "believes fox [were] introduced 25 years ago by Dave and Don Henry on Butler's knob [near Alger Mountain]". In addition, according to Brooks (1930) in a report on the larger mammals of the Mt. Baker National Forest, which covered much of Whatcom, Skagit, and Snohomish Counties, red foxes were "absolutely unknown up to about 1910. Now common."

Subsequent introductions were apparently made on two of the larger islands in Puget Sound. Mr. Squires reported that "in 1912 or 1914, five of the original stocking were live-trapped and released on Whidbey Island [in Island Co.]. Prior to this time, it is reported that there were no fox on this island. . . . Subsequent trappings and releases were made on San Juan Island [in San Juan Co.]." Schoen (1972) reported that red foxes were introduced on San Juan Island in an attempt to control an irruptive population of European rabbits (*Oryctolagus cuniculus*). A man named Osburn, who was the Extension Agent for San Juan Co., informed him that a pair of red foxes was introduced in 1947, and that others were brought in during the following years. In 1972, red foxes were apparently nearing extinction on the Island. Trapping records of the State Dept. of Game further illuminate that situation (Table 1). One red fox was taken from San

TABLE 1. Summary in five-year blocks of the harvest of red foxes in Washington west of the Cascade Crest, as reported by licensed trappers between 1938 and 1980. Data from Washington State Department of Game.

County	1938-1942	1943-1947	1948-1952	1953-1957	1958-1962	1963-1967	1968-1972	1973-1977	1978-1980	Total
Whatcom	77	115	26	32	70	7	83	17	3	505
Skagit	115	291	30	84	64	82	73	53	15	807
Snohomish	31	78	28	58	74	85	25	10	1	390
King	1	4	1	1	2	4	14	20	7	54
Pierce	4	2	7	1	24	23	61	26	16	164
Lewis	7	2	1	3	38	16	7	15	1	90
Skamania	1	0	0	0	0	0	5	3	0	9
Clark	0	0	2	2	0	1	0	5	3	13
Cowlitz	0	0	0	2	2	0	12	13	3	32
Wahkiakum	0	1	0	0	1	0	1	0	0	3
Pacific	0	0	0	0	1	0	14	0	0	15
Grays Harbor	0	1	0	5	17	16	25	4	3	71
Thurston	1	19	20	15	4	9	40	22	17	155
Mason	0	0	3	1	5	27	14	35	13	98
Kitsap	0	0	3	0	5	34	53	94	33	222
Jefferson	0	0	0	0	0	0	0	25	63	88
Clallam	0	0	0	5	6	27	5	48	23	114
Island	0	0	0	2	23	33	20	285	46	409
San Juan	1	2	0	0	5	26	143	0	0	177

Juan Co. in 1942, and two in 1947. These probably represent animals remaining from the original stocking. From 1948 to 1959, no foxes were taken on the Island. After that, presumably when the population began to build up again after the second introduction, foxes were trapped in increasing numbers until in 1968, 1969, and 1970 there were 25, 83, and 35 animals taken, respectively. None has been reported after that.

Whether red foxes are extinct on San Juan Island, or simply at the low end of a population cycle, is not known.

Mr. Andy Rogers of Seabeck, Washington, in Kitsap Co., a trapper of over 40 years' experience, informed me that "foxes were unheard of [in Kitsap Co.] until they began to be sighted . . . shortly after World War II. Some years ago, in a conversation with Bill Glud of Brownsville, I learned that he and Russell Root of Fernwood . . . had released foxes here thinking they might be good game for hound hunting." He was not told, however, where these foxes had originated.

The escape or release of red foxes from fur farms has also been an important mechanism of introduction. Mr. Squires stated that "in 1920, a fox farm was started at Bay View Ridge [in western Skagit Co.]. The population being comprised of both . . . blue and silver [foxes]. Some of these escaped and it is reported that they mated with the already established population of [introduced] red fox." Mr. Bill Hoffman of Concrete, Washington, a retired employee of the State Dept. of Game, informed me that in the early 1950s he trapped a silver fox that had a brand on it, indicating that it had escaped from a fur farm. He believed this animal came from a farm that had operated in the 1940s near Ferndale in western Whatcom Co. Presumably, when fur prices significantly declined in the early 1950s, the animals at this farm were turned loose. During this period, the average pelt-price for red foxes in Washington dropped to a low of $0.65 (Fig. 2), which no doubt rendered fox farming uneconomical.

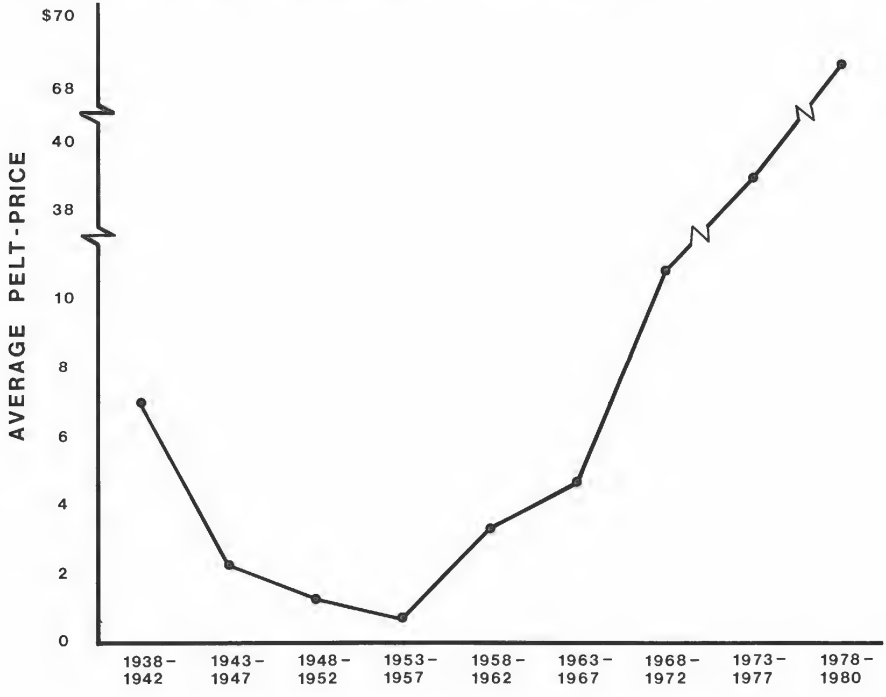

Figure 2. Average pelt-price for red fox in Washington between 1938 and 1980. No data available for 1942, 1943, 1945, or 1950. Data from Washington State Department of Game.

The presence of a fur farm in the southern Puget Sound region in the 1930s is indicated by a museum specimen that was obtained from a silver fox farm near Tacoma in western Pierce Co. in December 1933 (Mus. Nat. Hist., Univ. Puget Sound, specimen no. 522). In addition, Sid Hayes of Twisp, Washington, a native of Yelm in eastern Thurston Co., reported that "a neighbor . . . Roy Shearer . . . raised red fox. About 1920 or 1922, a bunch of his foxes dug under [the] fence. Before that time, I'd never [seen] a fox in Washington . . . or spoke to anyone who had. I do know that they became quite plentiful in the coast area after that. . . ." John and Stuart Keatley of Castle Rock, Washington, ran a silver fox farm just above the mouth of the Toutle River in Cowlitz Co. from the 1930s to the 1970s. According to one of the owners, however, none of their animals ever escaped.

The only records of fox farms on the Olympic Peninsula were in northeastern Clallam Co. Mr. Dowell Hilt, of Port Angeles, Clallam Co., and a retired mink rancher, reported that there were two fox farms in this region. One was a farm at McDonald Creek that raised silver fox breeders in the 1930s and 1940s. According to Mr. Hilt, these foxes were worth thousands of dollars at the time, and it is unlikely that any escaped or were released. The other was operated by Mr. Milo Rice on the Dungeness River from about 1938 to 1958. He raised several color phases, including red, platinum, silver, and gray (probably cross). They escaped frequently, and he reportedly also let many go. According to Mr. Hilt, wild foxes were not present before this farm began operating. State trapping records (Table 1) and historical reports support this assertion. Red foxes were not trapped in Clallam Co. until 1955. In Jefferson Co., which is situated south and east of Clallam Co., however, red foxes were not reported by trappers until 1974, indicating that red foxes did not colonize the northern Olympic Peninsula from the mainland to the south, where they had been common for some time, but that they originated in Clallam Co. and subsequently moved into the coastal areas of eastern Jefferson Co. Scheffer (1949) conducted a survey of mammals on the Olympic Peninsula in the late 1940s and reported that red foxes did not occur there. By the early 1950s that situation remained unchanged (Johnson and Johnson 1952).

Fox farms were also in operation on the east side of the Cascades. According to Mr. Russell Thompson of Thorp, Kittitas Co., a former Federal trapper and employee of the State Dept. of Game, three fox farms were in operation in Kittitas Co. in the 1930s and 1940s. One was in the northern part of the county near Liberty in the foothills of the Wenatchee Mountains, the other two in the vicinity of Ellensburg in southern Kittitas Co. C. E. McFarland, who was interviewed by Scheffer (1938), reported "there are a few [red foxes] between Cashmere and Leavenworth [in southern Chelan Co.], mostly blacks. Silvers occasionally escape from farms."

Mr. Bob Lynds of Colville, Stevens Co., reported that a fox farm was operated four miles north of Colville in the 1930s and 1940s by a man named Mottler. In 1942, Mr. Lynds trapped two tame silver foxes that had escaped from the fur farm. Upon contacting Mr. Mottler, he learned that a few foxes escaped every year. According to Mr. Lynds, whose father and grandfather began trapping northeastern Washington before 1900, there were no red foxes in that area before this farm came into operation.

The average pelt-price for red foxes in Washington has risen sharply since the late 1960s (Fig. 2). Apparently, this increase has once again stimulated interest in fox farming. I am aware of three farms currently operating in the State: at Cle Elum in

central Kittitas Co., since 1981; in the Cathcart area of southwestern Snohomish Co., since 1977; and at Graham in western Pierce Co., during the last few years. There is no indication that any foxes have escaped or been released from these farms.

Present Distribution

Distribution records of red foxes in Washington, which include State and Federal records, museum specimen localities and records gathered from correspondence with trappers, are shown in Fig. 3. All records are included, except for the area contained

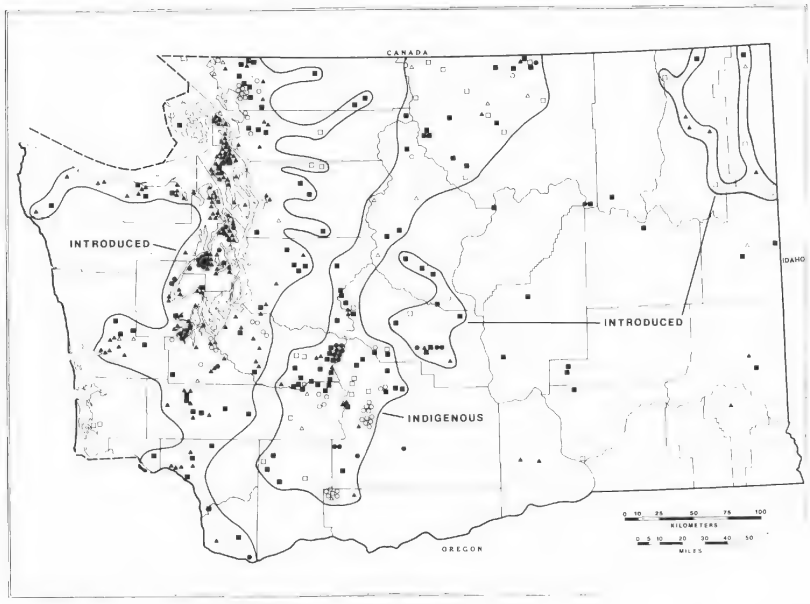

Figure 3. Distribution records and geographic ranges for indigenous and introduced populations of red foxes in Washington. Squares represent sight reports; triangles, trapping records; and circles, locality records of museum specimens. Hollow symbols indicate records dated prior to 1970.

within Mt. Rainier National Park. There are over 140 sight records from the Park dating back to 1897. Consequently, I have indicated only those records that represent different areas where foxes have been sighted. It is noteworthy that only three of these records came from the north or west side of Mt. Rainier, and of these, only one was made since 1970.

On the basis of these records, geographic ranges were drawn for existing populations of red foxes (Fig. 3). A widely distributed population of introduced red foxes occurs throughout the lowlands west of the Cascade Mountains. These foxes inhabit farmlands, the coastal areas of Puget Sound and the Strait of Juan de Fuca, and developed river valleys in the western foothills of the Cascade Mountains. Areas that are apparently

unsuitable for introduced red foxes in western Washington include the dense forests of the Cascades, the Willapa Hills in southwestern Washington, the outer coast zone, and the forests and subalpine meadows of the Olympic Mountains.

The range of the Cascade red fox differs somewhat from that shown on distribution maps published previously (Booth 1947, Dalquest 1948, U.S. Army Corps of Engineers 1974). Because of the presence of high mountains in central and eastern Whatcom Co., most notably Mt. Baker, this area has been included within the range of the Cascade fox. This region, however, is cut off from the main Cascade chain by the deep valley of the Skagit River, and no records of red foxes from high elevations have been reported from this area. Presumably, this river acts as a barrier to the movements of Cascade foxes and, as a result, the only red foxes present are introduced animals that have moved into the area along river valleys and highways. In addition, the eastern boundary of the range of the Cascade fox has typically been drawn to include portions of the Columbia Basin to accommodate distributional records that are, in fact, representative of introduced populations.

In the southern end of their range, Cascade foxes inhabit extensive areas west of the Cascade Crest. Appropriate habitat on two volcanoes, Mt. St. Helens in northwestern Skamania Co. and Mt. Rainier, account for these distributional records. Unlike the situation in the Mt. Baker area, there is no barrier to the movement of Cascade foxes between these areas and the meadows near the Cascade Crest.

Since most records of lowland red foxes were gathered during the course of this study, it is not possible to determine whether range expansion or contraction has occurred for introduced foxes in recent years. Many historical records for the Cascade fox exist, however, and these are indicated by hollow symbols in Fig 3. Comparing these records with those dated since 1970 (indicated by solid symbols), it is evident that no significant changes in distribution have occurred in recent years. Cascade foxes were present on the slopes of Mt. St. Helens, but their population status following the May 1980 eruption is unknown.

At mid-elevations, the western slope of the Cascades is characterized by dense, wet forests dominated by western hemlock, *(Tsuga heterophylla)* and Douglas fir *(Pseudotsuga menzeisii)* with a lush understory (Franklin and Dyrness 1973). This habitat appears to be unsuitable for both the Cascade and lowland populations, probably because red foxes are cursorial predators favoring open meadows for hunting small rodents, their principal prey (Bailey 1936b). Consequently, west of the Cascade Crest, introduced and indigenous populations of red foxes are separated by a belt of dense coniferous forest. Red foxes would be capable of crossing this uninhabited zone, because these forests do not present a physical barrier to their movements. Introduced foxes have not colonized the subalpine meadows of the Olympic Mountains, even in the absence of competition from native foxes. This observation indicates that introduced red foxes are restricted to habitat at low elevations by physiological or behavioral limitations and provides strong evidence that introduced red foxes have not invaded the meadows at upper elevations in the western Cascades to interbreed with native foxes. Apparently, such limitations have also operated to restrict indigenous red foxes to habitat at high elevations.

Cascade red foxes clearly favor the eastern slope of the Cascade Range. At mid-elevations, annual precipitation is much lower than on the western side, the forests are

drier and the understory less dense. Dominant forest species are principally grand fir *(Abies grandis)* and ponderosa pine *(Pinus ponderosa)* (Franklin and Dyrness 1973). Because the east-side forests are open, they probably provide enough space for cursorial predators to effectively exploit available prey, whereas the dense forests at similar elevations on the western slope do not.

The red fox is reportedly absent from the Columbia Basin east of the Cascades (Dalquest 1948, Larrison 1970). Information gathered from trappers, however, indicates that foxes are infrequently found in this region. The river valleys and populated areas of central Kittitas and southern Chelan Counties appear to support a sizeable population that is presumably derived from foxes that escaped from fur farms in the 1930s and 1940s. The other scattered reports from the Columbia Basin probably represent wandering or dispersing individuals, because the great majority of trappers from those areas have reported never sighting or trapping a red fox.

On the east side of the Cascades, unlike the west, no wide buffer zone of uninhabited forest separates indigenous and introduced populations of red foxes. Consequently, these populations are nearly parapatric in Chelan and Kittitas Counties, and it is here that hybridization would most likely occur. Assessment of this possibility, however, must await collection of an adequate series of specimens.

The presence of red foxes in the highlands of northeastern Washington has long been recognized. This population has been assigned to both the Rocky Mountain (Dalquest 1948) and Cascade (Booth 1947) sugspecies. All records, however, are from developed sites at low elevations along river valleys. A game-mammal census conducted in 1925 on the Colville National Forest in northeastern Washington made no mention of red foxes (Anonymous 1925). A similar census five years later, estimated a population of five foxes (Anonymous 1931). These facts, along with the information provided by Mr. Lynds on the introduction of farm foxes into this area, provide strong evidence that this population is descended from introduced animals.

TABLE 2. Summary in five-year blocks of the harvest of red foxes in Washington east of the Cascade Crest, as reported by licensed trappers between 1938 and 1980. Data from Washington State Department of Game.

County	1938-1942	1943-1947	1948-1952	1953-1957	1958-1962	1963-1967	1968-1972	1973-1977	1978-1980	Total
Asotin	0	0	0	0	0	0	0	0	0	0
Garfield	0	0	0	0	0	0	0	0	0	0
Columbia	0	0	0	0	0	0	0	0	0	0
Walla Walla	0	0	0	0	0	0	0	0	0	0
Benton	12	0	0	0	0	0	0	1	1	14
Franklin	0	0	0	0	0	0	0	0	0	0
Douglas	0	0	0	0	1	0	0	0	0	1
Grant	0	0	0	0	0	0	1	0	0	1
Adams	0	0	0	0	0	0	1	0	0	1
Whitman	0	0	0	0	0	0	2	0	0	2
Lincoln	0	0	0	0	0	0	0	0	0	0
Spokane	0	1	0	0	0	2	1	0	0	4
Pend Oreille	0	2	0	0	0	0	0	6	1	9
Stevens	0	0	0	0	0	0	0	0	0	0
Ferry	2	0	0	0	0	0	0	0	0	2
Okanogan	6	4	5	2	0	1	1	0	0	19
Chelan	5	2	0	0	0	1	0	0	0	8
Kittitas	17	3	4	2	5	21	37	21	8	118
Yakima	16	12	0	0	1	0	5	0	1	35
Klickitat	8	10	0	0	4	0	0	1	0	23

The Blue Mountains in southeastern Washington have consistently been included within the range of the Rocky Mountain red fox (Booth 1947, Dalquest 1948, Hall 1981). In 1923, a red fox was collected from the Blue Mountains of Washington (Nat. Mus. Natur. Hist., specimen no. 244010), although no specific collecting locality was recorded. This specimen constitutes the only evidence that indigenous red foxes occur in southeastern Washington. The one other record of a red fox from this area came from a ploughed field at the base of the Blue Mountains in Garfield Co. (Fig. 3). Numerous trappers, many of whom have trapped for decades, consistently reported that red foxes do not occur in the Blue Mountains. As shown in Table 2, red foxes have not been reported by trappers in any of the four counties that encompass the Blue Mountains (Asotin, Garfield, Columbia, and Walla Walla). It is evident that these were wandering foxes that were not from an established local population.

Because the geographic origins of the introduced red fox in Washington are largely unknown and probably diverse, assignment of these populations to established subspecies is unwarranted. It is also doubtful that anything significant can be gained by granting unique subspecific status to introduced populations of red foxes in Washington.

Acknowledgments

This investigation was supported through funds granted by the Washington State Department of Game as part of Study No. 4, Project No. E-1. The Department of Game also provided access to trapping records and sight reports and their cooperation during the course of this study is appreciated. This research was in partial fulfillment of my Ph.D. degree at the College of Forest Resources, University of Washington. I am grateful to Dr. Richard D. Taber, the chairman of my graduate committee, for advice and support. I am also indebted to Drs. Stephen D. West, Robert L. Rausch, Sievert A. Rohwer and Murray L. Johnson, and to Stephanie Livingston and Carol A. Apruzzese for reading early drafts of the manuscript and offering valuable suggestions. I am especially grateful to the members of the Washington State Trappers Association, without whose help this work could not have been completed. The following museums provided specimen locality records from Washington: Thomas Burke Memorial Washington State Museum, University of Washington, Seattle; National Museum of Natural History, Washington D.C.; Museum of Natural History, University of Puget Sound, Tacoma, Washington; Charles R. Conner Museum, Washington State University, Pullman; National Museum of Natural Sciences, Ottawa, Ontario; Denver Collection of the Bird and Mammal Laboratories, U.S. Fish and Wildlife Service; Battelle Northwest, Hanford, Washington; and the private collection of Arthur Peck, Jr., Ellensburg, Washington.

Literature Cited

Anonymous. 1925. Animal census in Colville National Forest, Washington. Murrelet 6: 5.

———. 1931. Wild game census in Colville National Forest, northeastern Washington. Murrelet 12: 26.

Bailey, V. 1936a. The red fox in America. Nature 28: 269-272, 317.

———. 1936b. The mammals and life zones of Oregon. N. Amer. Fauna 55: 1-416.

Booth, E. S. 1947. Systematic review of the land mammals of Washington. Unpubl. Ph.D. dissert., Wash. State Univ., Pullman.

Brooks, A. 1930. Early big game conditions in the Mount Baker district, Washington. Murrelet 11: 65-67.

Choate, J. R., and H. H. Genoways. 1975. Collections of Recent mammals in North America. J. Mamm. 56: 452-502.

Dalquest, W. W. 1948. Mammals of Washington. Univ. Kans. Publ. Nat. Hist., 2.
Fichter, E., and R. Williams. 1967. Distribution and status of the red fox in Idaho. J. Mamm. 48: 219-230.
Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech, Rep. PNW-8.
Gray, R. L. 1977. Extension of red fox distribution in California. Calif. Dept. Fish and Game 63: 58.
Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. Fur-bearing Mammals of California. Univ. Calif. Press, Berkeley.
Hall, E. R. 1981. The Mammals of North America. Second ed., J. Wiley and Sons, New York.
Ingles, L. G. 1965. Mammals of the Pacific States. Stanford Univ. Press.
Johnson, M. L., and S. Johnson. 1952. Checklist of mammals of the Olympic Penninsula. Murrelet 33: 32-37.
Larrison, E. J. 1970. Washington Mammals, Their Habitats, Identification and Distribution. Seattle Audubon Soc.
Lauckhart, J. B. 1970. Rare Mammals of Washington. Wildl. Soc., Wash. Chap.
———. 1972. The Red Fox in the Northwest. Unpubl. manuscript.
Livezey, R., and F. Evenden. 1943. Notes on the Western red fox. J. Mamm. 24: 500-501.
Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981. Natural history of Oregon Coast mammals. U.S. For. Serv. Gen. Tech. Rep. PNW-133.
Scheffer, V. B. 1938. Unpubl. field notes.
———. 1939. Unpubl. field notes.
———. 1949. Mammals of the Olympic National Park and Vicinity. Unpubl. manuscript.
Schoen, J. W. 1972. Mammals of the San Juan Archipelago: distribution and colonization of native land mammals and insularity in three populations of *Peromyscus maniculatus*. Unpubl. M.S. thesis, Univ. Puget Sound, Tacoma.
United States Army Corps of Engineers. 1974. Washington Environmental Atlas. Second ed., U.S. Govt. Print. Office, Wash., D.C.
Washington State Department of Game. 1976-1980. Individual trapper's reports of catch.

Received March 19, 1982
Accepted for publication May 3, 1982

Meetings

The Animal Behavior Society will hold its 1984 annual meeting (13-17 August) at Eastern Washington Univ., Cheney, Wash. Program information may be obtained from Lee C. Drickamer, Biology Dept., Williams College, Williamstown, Mass. 01267. Information on registration and housing may be obtained from Steven B. Christopher, Office of Academic Affairs, Showalter Hall, Eastern Washington Univ., Cheney, Wash. 99004.

The 1984 annual meeting of The American Ornithologists' Union will be held 5-10 August at the Univ. of Kansas, Lawrence.

1983 Manuscript Reviewers

The editorial staff and the Association thank the following people for serving as manuscript referees during the past year:

E. G. Bizeau, D. W. Bushaw, I. O. Buss, J. A. Byers, E. P. Catts, R. del Moral, C. Driver, J. R. Dunn, T. Fleming, W. H. Funk, D. P. Furman, H. L. Gibbons, A. J. Gilmartin, D. Helvey, E. Hindin, D. L. Johnstone, A. Kendall, J. O. Klemmedson, E. Kozloff, W. Lopuskinsky, R. Mack, D. Medin, E. H. Merrill, D. L. Nelson, J. R. Nelson, F. W. Rabe, R. Rice, T. L. Righetti, S. W. Running, L. A. Sharp, C. Slaughter, M. V. Stalmaster, E. H. Stauber, N. Stark, K. Swedberg, J. M. Taylor, R. J. Taylor, D. W. Uresk, E. S. Verry, L. Volland, E. B. Welch, S. N. Wiemeyer, C. Williams, and D. Zobel.

Paul C. Fielder[1]

and

Charles E. McKay, Jr.

Applied Wildlife Ecology
Washington Department of Game
3860 Chelan Highway
Wenatchee, Washington 98801

Vegetation Types Used by Mule Deer Fawns, Mid-Columbia River, Washington

Abstract

Mule deer *(Odocoileus hemionus)* fawn surveys were conducted by boat along the Columbia River in north-central Washington from June through August, 1977-79. A total of 288 fawn observations was made in 12 vegetation types. Four vegetation types totaled 7.1 percent of the study area but accounted for 69 percent of the fawn observations. The shrub steppe vegetation type comprised 68.1 percent of the study area but accounted for only 27.1 percent of the observations. Fawns preferred vegetation types that provided both a shade producing overstory and a shrub understory. Protection from the summer heat, and possibly predators, may influence selection of vegetation types.

Introduction

Vegetation types used by mule deer *(Odocoileus hemionus)* fawns are important for survival, but information on vegetation requirements is limited (Sheehy 1978). Does may influence selection of the general area and thus the vegetation types that fawns use. The extent of this influence on exact use areas, especially where several vegetation types are in close proximity, is unknown. White-tailed deer *(Odocoileus virginianus)* fawns appear to select bedding and other use areas without assistance from the doe (Jackson *et al.* 1972). Mule deer fawns probably do so also. Selection of use areas by fawns may imply preference for or avoidance of vegetation types (Martinka 1968, Suring and Vohs 1979).

This paper discusses vegetation types used and the types avoided by mule deer fawns during summer along the mid-Columbia River in north-central Washington. The importance of habitat or plant species preference and avoidance by wildlife is recognized (Neu *et al.* 1974, Hirst 1975, Collins *et al.* 1978, Stalmaster and Newman 1978, Taylor and Guthery 1980, Cairns and Telfer 1980, Wiseman and Lewis 1981, Tilton and Willard 1982). Habitat changes along the Columbia River resulting from increasing agriculture, livestock grazing, and modifications at hydroelectric dams may force wildlife managers to give special attention to protect and increase preferred vegetation types.

Study Area

The study area includes the land within 402 m of the 72.4 km section of the Columbia

[1]Present address: Fish & Wildlife Operations, Chelan County P.U.D. P.O. Box 1231, Wenatchee, Washington 98801.

River between Chief Joseph Dam and rivermile 590 in north-central Washington. Douglas County and the Colville Indian Reservation in Okanogan County border the south and north shores, respectively.

The climate of the study area is semi-arid. Summer temperatures average 23.9°C. Annual precipitation averages 240 mm, with about 13 mm per month during the summer.

The study area is characteristic of the Upper Sonoran life zone, with stands of deciduous and coniferous trees scattered along the river. Erickson *et al.* (1976) described 12 vegetation types within the 7368 ha study area and calculated acreages by identification in the field, delineation on aerial photos, and the dot-grid method (Table 1). The

TABLE 1. The amounts and occurrence of the 12 vegetation types and their summer use by mule deer fawns along the mid-Columbia River, Washington, 1977-79.

Vegetation Type	No. of separate units	Avg. size of each unit (ha)	Availability: Total area (ha)	Availability: % of total area	Utilization: Fawn Observations: no.	Utilization: Fawn Observations: %	Apparent Selection[1] Behavior
Conifer over shrub	40	4.5	105.4	2.5	110	38.2	Preference
Rockland	12	18.6	223.8	3.0	48	16.7	Preference
Macrophyllus vine and shrub	41	1.6	74.5	1.0	33	11.5	Preference
Riparian	33	1.2	42.5	0.6	8	2.6	Preference
Mixed decidious and conifer tree over shrub	5	3.6	10.6	0.2	3	1.0	None[2]
Deciduous tree over shrub	28	1.6	46.5	0.6	3	1.0	None
Island	6	12.1	74.1	1.0	4	1.3	None
Conifer forest	13	6.1	79.7	1.1	0	0.0	None
Shrub steppe	31	163.9	5,078.1	68.1	78	27.1	Avoidance
Agricultural	36	20.6	739.8	9.9	1	0.3	Avoidance
Rock	60	7.3	447.2	6.0	0	0.0	Avoidance
Development	13	34.4	446.0	5.9	0	0.0	Avoidance

[1]$P<0.05$.
[2]None indicates use was not significantly different from availability.

dominant trees, shrubs, and grasses or forbs of the 12 vegetation types are listed in Table 2.

About 175-200 mule deer summer within the study area. Coyotes *(Canis latrans)* and Golden Eagles *(Aquila chrysaetos)* are common predators, and several bobcats *(Lynx rufus)* also occur in the area.

Methods

Vegetation types, rather than habitat types, were the most meaningful classification for this study. Vegetation type is a classification based on what actually occupies an area (Daubenmire 1952).

Fawns were counted during 30 boat surveys conducted during the last week of June through August, 1977-79. These surveys were essentially a strip census along each shore of this portion of the river. Both shores were sampled from an average distance of 30 m during each survey. This distance allowed equal proximity to all vegetation types and reduced observability bias of the different vegetation types to a level we believed to be negligible. One shore was observed on the upstream trip and the other on the downstream trip. The shores observed on the upstream and downstream trips were alternated every survey. Surveys were usually conducted from dawn to dusk to incdlude all activity periods of fawns (Jackson *et al.* 1972). We located fawns either by direct

TABLE 2. Dominant trees, shrubs, and grasses or forbs of the 12 vegetation types in the study area[1].

Vegetation type	Tree	Shrub	Grass or forb
Conifer over shrub	**Pinus ponderosa**	**Amelanchier alnifolia** **Philadelphus lewisii**	**Bromus tectorum** **Festuca idahoensis**
Rockland		**Artemisia tripartita** **Artemisia tridentata**	**Festuca idahoensis** **Bromus tectorum**
Macrophyllous vine and shrub		**Amelanchier alnifolia** **Clematis ligusticifolia**	**Bromus tectorum** **Festuca idahoensis**
Riparian	**Betula occidentalis**	**Symphoricarpos alba** **Philadelphus lewisii**	**Equisetum arvense** **Equisetum hemale**
Mixed deciduous and conifer tree over shrub	**Pinus ponderosa** **Betula occidentalis**	**Philadelphus lewisii** **Symphoricarpos alba**	**Bromus tectorum** **Festuca idahoensis**
Deciduous tree over shrub	**Populus trichocarpa** **Betula occidentalis**	**Crataegus columbiana** **Philadelphus lewisii**	**Bromus tectorum** **Elymus glaucus**
Island	**Juniperus scopulorum** **Pinus ponderosa**	**Purshia tridentata** **Amelanchier alnifolia**	**Artemisia ludoviciana** **Poa pratensis**
Conifer forest	**Pseudotsuga menziesii** **Pinus ponderosa**	**Purshia tridentata** **Ribes cereum**	**Bromus tectorum** **Festuca idahoensis**
Shrub steppe		**Artemisia tridentata** **Purshia tridentata**	**Bromus tectorum** **Festuca idahoensis**
Agricultural	Orchards, vineyards, hay, and cereal grains		
Rock		**Clematis ligusticifolia** **Philadelphus lewisii**	**Bromus tectorum** **Agropyron spicatum**
Development	Ornamental (park-like) trees and shrubs or no vegetation		

[1]Information from Erickson **et al.** (1976).

observation or, if an observed doe's behavior indicated that a fawn was present, by a ground search. Diem (1954) found that when a mule deer fawn was present, its dam would usually trot off a short distance and stop, act irritated, stamp her feet, switch her tail vigorously, and hestitate to leave the area. We found that this behavior was a reliable indicator of fawn presence. We used a predator call to flush several fawns, as suggested by Diem (1954).

Preference and avoidance of the vegetation types were determined by comparing their availability to utilization. A Chi-square test ($P<0.05$) was used to test the hypothesis that fawns occurred in vegetation types in proportion to those types available in the study area (Neu *et al.* 1974, Tilton and Willard 1982). We presented results in a format similar to that used by Tilton and Willard (1982), although other presentations of preference and avoidance data (Marion and Ryder 1975, Stalmaster and Newman 1979, Taylor and Guthery 1980, Wiseman and Lewis 1981) could also be applied to our data with similar results.

Results

We made 288 observations of approximately 139 mule deer fawns. The number of fawns was estimated from the small home range of fawns (Steigers 1978, 1981; Geduldig 1981), location along the river, and group size. Although the vegetation types were scattered randomly along both shores, 94 percent of the observations were on the north-facing, Douglas County shore. Several differences between the two shores, not related

to vegetation types, probably influenced this distribution. These differences are discussed later.

The proportion of fawn observations in each vegetation type differed significantly from the availability of those types in the study area (Chi-square calculated = 2145; tabular value 11 df, 0.05 level of probability = 19.675). The null hypothesis was therefore rejected, implying fawns used vegetation types disproportionately to the availability of those types (Table 1). Fawns preferred the conifer over shrub, macrophyllous vine and shrub, rockland, and riparian types. These four vegetation types totaled only 7.1 percent of the study area but accounted for 69 percent of the fawn observations. Fawns avoided development, rock, agricultural, and shrub steppe vegetation types. Shrub steppe had the highest availability of all vegetation types within the study area (68.1 percent of the total area) but accounted for only 27.1 percent of the fawn observations.

Discussion

All of the vegetation types that fawns preferred, except rockland, had an overstory of trees or relatively tall shrubs and a thick understory of shrubs. These characteristics are also important components of fawning and summer habitats for fawns in western Okanogan County (Zeigler 1978), eastern Oregon (Sheehy 1978), and western South Dakota (Steigers 1981). All of the vegetation types avoided lacked this combination of overstory and understory.

Rockland and shrub steppe vegetation types were similar, except that the former had numerous large, haystack-shaped basalt rocks scattered throughout. These types provided microhabitat variations, including shade and increased moisture, which promoted succulent vegetation. We often saw fawns in the shade of these rocks and believe the rocks may have provided the function of an overstory.

Avoidance of the shrub steppe vegetation type by fawns is important. If visability bias between the vegetation types existed, one would expect that deer using the more open shrub steppe type would be more readily observed. Apparently this large vegetation type does not meet the daytime needs of mule deer fawns.

If ungulates display no preference for any particular habitat, their distribution over a selected area containing these habitats should be about even. However, animals exhibiting a heterogeneous distribution over a given area are responding to habitat factors that relate directly or indirectly to their well-being and survival (Hirst 1975). Mule deer fawns prefer vegetation types with an overstory and shrub understory diurnally during the summer along the mid-Columbia River. Overstory importance may relate to protection from high summer temperatures (Steigers 1981) and/or moisture retention. The fact that 94 percent of the fawns were seen on the north-facing bank, which escapes the sun's direct rays and has a cooler microclimate, supports this idea. However, a road and long hunting seasons (six months for bucks and three months for does) on the north bank probably also influenced north bank-south bank distribution of all deer in the study area. An understory of shrubs may provide concealment from predators (Barrett 1981). Whatever the reasons, the combination of a shade producing overstory and a shrub understory seems to be what mule deer fawns prefer here diurnally during summer. Deer managers of arid areas used for fawning and by summering mule deer may

wish to give special consideration to vegetation types with such overstory-understory combinations by protecting existing stands and promoting the growth of new stands.

Acknowledgments

The U.S. Fish and Wildlife Service, Ecological Services, Olympia, Wash., and U.S. Army, Corps of Engineers, Seattle District, funded this study as a part of fish and wildlife studies associated with Chief Joseph Dam. Joe Foster, Rick Knight, and Don Zeigler provided comments on drafts of this manuscript.

Literature Cited

Barrett, M. W. 1981. Environmental characteristics and functional significance of pronghorn fawn bedding sites in Alberta. J. Wildl. Manage. 45: 120-131.

Cains, A., and E. Telfer. 1980. Habitat use by four sympatric ungulates in boreal mixedwood forest. J. Wildl. Manage. 44: 849-857.

Collins, W., P. Urness, and D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. J. Wildl. Manage. 42: 799-810

Daubenmire, R. F. 1952. Forest vegetation of northern Idaho and adjacent Washington and its bearing on concepts of vegetation classification. Ecol. Monog. 22: 301-330.

Diem, K. L. 1954. Use of a deer call as a means of locating deer fawns. J. Wildl. Manage. 18: 537-538.

Erickson, A., Q. Stober, . Brueggeman, and R. Knight. 1976. An assessment of the impact on the wildlife and fisheries resource of Rufus Woods Reservoir expected from the raising of Chief Joseph Dam from 946 to 956 ft. m.s.l. College of Fisheries, Univ. of Washington, Seattle.

Geduldig, H. L. 1981. Summer home range of mule deer fawns. J. Wildl. Manage. 45: 726-728.

Hirst, S. M. 1975. Ungulate-Habitat Relationships in a South African Woodland/Savanna Ecosystem. Wildl. Monogr. No. 44.

Jackson, R., M. White, and F. Knowlton. 1972. Activity patterns of young white-tailed deer fawns in south Texas. Ecology 53: 262-270.

Marion, W., and R. Ryder. 1975. Perch-site preferences of four diurnal raptors in northeastern Colorado. Condor 77: 350-352.

Martinka, C. J. 1968. Habitat relationships of white-tailed and mule deer in northern Montana. J. Wildl. Manage. 32: 558-565.

Neu, C., C. Byers, and J. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38: 541-545.

Sheehy, D. 1978. Characteristics of Shrubland Habitat Associated with Mule Deer Fawns at Birth and During Early Life in Southeastern Oregon. Infor. Rep. Series, Wildlife 78-1. Oregon Dep. Fish and Wildlife, Portland.

Stalmaster, M., and J. Newman. 1979. Perch-site preferences of wintering bald eagles in northwest Washington. J. Wildl. Manage. 43: 221-224.

Steigers, W. D. 1978. Mortality of Mule Deer Fawns in South-Central Washington. M. S. Thesis, Brigham Young Univ., Provo, Utah.

———, 1981. Habitat Use and Mortality of Mule Deer Fawns in Western South Dakota. Ph.D. thesis, Brigham Young Univ., Provo, Utah.

Suring, L., and P. Vohs, Jr. 1979. Habitat use by Columbian white-tailed deer. J. Wildl. Manage. 43: 610-619.

Taylor, M, and F. Guthery. 1940. Fall-winter movements, ranges, and habitat use of lesser prairie chickens. J. Wildl. Manage. 44: 521-524.

Tilton, M., and E. Willard. 1982. Winter habitat selection by mountain sheep. J. Wildl. Manage. 46: 359-366.

Wiseman, D., and J. Lewis. 1981. Bobwhite use of habitat in tall grass rangeland. Wildl. Soc. Bull. 9: 248-255.

Zeigler, D. L. 1978. The Okanogan Mule Deer. Biological Bull. No. 15, Washington Dep. Game, Olympia.

Received May 17, 1982
Accepted for publication August 26, 1982

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian D. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1984 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaueuser Company, Centralia, Washington

1984 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Oregon Institute of Technology, Klamath Falls, Oregon
Oregon State University, Corvallis, Oregon
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
Saint Martin's College, Lacey, Washington
Seattle Central Community College, Seattle, Washington
Seattle Pacific University, Seattle, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State University, Pullman, Washington
Western Oregon State College, Monmouth, Oregon
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1984 Sustaining Individual Members

R. Michael Anthony, Bend, Oregon
Stephen F. Arno, Florence, Montana
Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
Tim W. Clark, Jackson, Wyoming
Richard G. Cline, Missoula, Montana
Susan G. Conrad, Corvalis, Oregon
George W. Douglas, Victoria, British Columbia, Canada
Arlene T. Doyle, Arcata, California
George R. Fahnestock, Seattle, Washington
William R. Funk, Pullman, Washington
Tom Gnojek, Soda Springs Idaho
Gerald H. Haddock, Wheaton, Illinois
Frederick C. Hall, Portland, Oregon
Charles R. Hatch, Moscow, Idaho
Francis R. Herman, Fairbanks, Alaska
Robert J. Jonas, Moscow, Idaho
Barry L. Keller, Pocatello, Idaho
John H. Larsen, Pullman, Washington
Denis P. Lavender, Corvallis, Oregon
Cal E. Meier, College Station, Texas
Emmett B. Moore, Jr., Richland, Washington
William H. Rickard, Richland, Washington
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Ronald J. Taylor, Bellingham, Washington
Ralph L. Thompson, Berea, Kentucky
David D. Tillson, Salt Lake City, Utah
James M. Thorpe, Corvallis, Oregon
Daniel W. Uresk, Rapid City, South Dakota
Shepard M. Zedeker, Christiansburg, Virginia

Northwest Science

Information for Authors

The pages of *Northwest Science* are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. *Northwest Science* does not publish notes, letters, or bibliographic papers. Short papers are treated the same as longer manuscripts. All submissions are refereed, usually by two reviewers. Papers are also welcome from authors outside of the Pacific Northwest.

At least one of the authors of all papers considered for publication must be a member of the Northwest Scientific Association.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures)*; provide ample margins. Computer printouts are not acceptable. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, double-spaced and not exceeding five percent of the paper, should precede every article. The abstract should recapitulate the major points of the paper and should be suitable for use by abstracting services.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page.

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials*. Consult with the *Council of Biology Editors (CBE) Style Manual*, 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence should be between senior author and the Editor.

Editing—Manuscripts may be edited for grammatical correctness and clarity.

Galley Proofs and Reprints—One set of proofs will be sent to the senior author for correction shortly before publication; proofs should be returned to the Editor within three days of receipt. Senior authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs.

Page Charges—Page charges are currently $50 per printed page. Publication is not contingent upon payment of page charges, as the Association is prepared to assume them for members whose work is unsupported, but even partial payment would be helpful in order that we may continue this policy.

Non-Profit Org.

BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

US ISSN 0029 344X

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Editor John W. Weber Washington State University

Associate Editors

Botany	Robert L. Carr	Eastern Washington University
Chemistry and Physics	Frank L. Curzon	University of British Columbia
Engineering and Mathematics	Dale C. Perry	University of Idaho
Forestry	Warren P. Clary	U.S. Forest Service
Geology	Franklin F. Foit, Jr.	Washington State University
Social Sciences	Phillip D. Young	University of Oregon
Soils	Robert L. Edmonds	University of Washington
Zoology	Donald R. Johnson	University of Idaho

Papers published in *Northwest Science* are indexed in *Current Contents* and *Science Citation Index.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.

Volume 58, Number 2

May 1984

Northwest Science

CONTENTS

85 Chemical Content of Snow and Effect of Melting on Cascade Mountain Lakes
Eugene B. Welch, William H. Chamberlain, and Dimitris E. Spyridakis

94 Indian Basin Advance in Western and North-Central Wyoming
W. C. Mahaney

103 Lead Shot Ingestion in Waterfowl in Washington State, 1978-1979
Crystal J. Driver and Ronald J. Kendall

108 The Zonation of Mosses and Lichens Along the Salmon River in Idaho
Roger Rosentreter

118 Biology of Smallmouth Bass (**Micropterus dolomieui**) in Lake Sammamish, Washington
David E. Pflug and Gilbert B. Pauley

131 A Comparison of Structural Properties and Compositional Trends in Conifer Forests of Yosemite and Glacier National Parks, USA
Albert J. Parker

142 Parasitic mites of voles of the genera **Microtus** and **Clethrionomys** from Oregon
John O. Whitaker, Jr., and Chris Maser

151 Comments on an Apparent Sharp-Tailed Grouse Movement in Eastern Montana
Irven O. Buss

153 Lice (**Mallophaga and Anoplura**) from Mammals of Oregon
K. C. Emerson, Chris Maser, and John O. Whitaker, Jr.

162 Association News

163 Northwest Science Index; Meetings; Announcement

Quarterly Publication of the Northwest Scientific Association

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science*, is open to individuals for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 300 students or more $40. All other subscribers, $25 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

John W. Weber
Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164-2910

Officers of the Association

President Oscar Sziklai
University of British Columbia
Vancouver, B.C. (1985)*

Vice-President Ray A. Soltero
Eastern Wasington University
Cheney, Washington (1985)

Secretary Robert L. Carr
Eastern Washington University
Cheney, Washington (1984)

Treasurer Steven J. Brunsfeld
College of Forestry, Wildlife, and Range Sciences
University of Idaho
Moscow, Idaho 83843 (1986)

Past President Stephen F. Arno
USDA, Forest Service
Missoula, Montana (1985)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Black
University of British Columbia
Vancouver, British Columbia
(1985)

Lee E. Eddleman
Oregon State University
Corvallis, Oregon (1987)

William H. Emmingham
Oregon State University
Corvallis, Oregon (1987)

Donald Hanley
Washington State University
c/o University of Washington
Seattle, Washington (1986)

Warren Iliff
Washington Park Zoo
Portland, Oregon (1986)

Susan Kephart
Willamette University
Salem, Oregon (1986)

Hubertus Kohn
Western Washington University
Bellingham, Washington (1987)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

M. A. Radwan
U.S. Forest Service
Olympia, Washington (1987)

Steven R. Seavey
Lewis and Clark College
Portland, Oregon (1985)

George G. Spomer
University of Idaho
Moscow, Idaho (1987)

Robert Stockhouse
Pacific University
Forest Grove, Oregon (1986)

Kareen Sturgeon
Linfield College
McMinnville, Oregon (1985)

B. J. Verts
Oregon State University
Corvallis, Oregon (1986)

*Term of office expires in the year given in parentheses.

PRINTED QUARTERLY (FEBRUARY, MAY, AUGUST, AND NOVEMBER) BY THE WASHINGTON STATE UNIVERSITY PRESS, OFFICE OF PUBLICATIONS, PULLMAN, WASHINGTON 99164-5910.

Eugene B. Welch

William H. Chamberlain

and

Dimitris E. Spyridakis

Department of Civil Engineering
Environmental Engineering and Science
University of Washington
Seattle, Washington 98195

Chemical Content of Snow and Effect of Melting on Cascade Mountain Lakes

Abstract

Sulfate and nitrate content in snow cores collected in the spring of 1982 indicated that deposition of those ions is greater in the Cascade Mountains, downwind from the Seattle-Tacoma urban-industrial area, than in the Olympic Mountains. Snowmelt and iceout did not result in episodes of low pH and alkalinity in the three high lakes sampled. The minimum pH was 5.8 and neither pH nor alkalinity showed a seasonal trend following iceout, although specific conductance did decrease slightly. The lack of an acidification episode was not surprising because the pH of snow from a site near the studied lakes averaged 5.3. The snow was richer in cations than had been reported earlier in precipitation from the Cascades, even though sulfate concentrations were similar.

Chemical stratification was apparent in the surface 20 m layer of the lower elevation lake, while the upper 50 m of the highest elevation lake was similar in alkalinity content to that observed in snow. The intermediate elevation lake showed a slight tendency to stratify in the upper 50 m. These observations suggest that snowmelt water does not mix with the whole lake volume in these deep lakes with relatively low watershed:lake surface area ratios and low flushing rates as might be expected in lakes with more extreme characteristics.

Introduction

Washington's Cascade Mountain lakes have been classified as some of the most sensitive waters in the United States (Omernick and Powers 1982). Their low buffering capacity is due to the granitic and basaltic bedrock and thin soil development surrounding many of these high elevation lakes. Many have relatively small watersheds, and their basins are steep-sided. Thus, they would be expected to respond rather quickly to even small increases in acid deposition.

The acidity of precipitation reaching the Cascades is greater than might be expected normally. Logan (1980) reported a mean annual pH of 4.66 in precipitation collected at Stampede Pass and, more recently, Logan *et al.* (1982) reported a mean of 4.7 at Snoqualmie Pass for the first half of 1981. Dethier (1979) reported a mean value of 4.8 in an area of the Cascades, north of Stevens Pass. Wasem (1982) has observed even lower values (4.3) for the North Cascades. Powers and Rambo (1981) summarized existing precipitation data.

Some of the acidity in precipitation falling on the Cascades no doubt originates from anthropogenic sources in the Puget sound lowlands (Logan *et al.* 1982). However, there are natural sources also. Mount Saint Helens released nearly three times as much sulfur dioxide, for three months following its eruption in May 1980, as normally originates from anthropogenic sources (PSAP 1980). Emissions had decreased considerably

by 1981 (Casadevall *et al.* 1981). Although the normal pH of precipitation saturated with carbon dioxide is 5.6, sulfate aerosols also exist naturally and, when scavanged by precipitation, can result in lower than "normal" pH. Charlson and Rodhe (1982) have suggested that without anthropogenic sources the precipitation pH could range between 4.5 and 5.6. They suggest that productive parts of the ocean may be a source for natural acidity.

Thus, there is the question of the relative contribution of anthropogenic and natural sources to the acidity of precipitation reaching the Cascades. Also, there are the associated questions of whether there is or has been detectable acidification of any lakes and what the nature of response would be in these lakes to incremental increases in acid deposition. Results reported here are based on the chemical content of snow cores collected in the spring of 1982 in the Olympic and Cascade Mountains and subsequent observations on changing chemical content of three highly sensitive Cascade lakes following iceout. The lakes are Angeline, Big Heart, and Copper and lie in the Alpine Lakes Winderness area at 1219 to 1555 m elevation between Snoqualmie and Stevens Passes. The objectives were to 1) determine if deposition of acid and the associated ions, sulfate and nitrate, is greater in the Cascades than the Olympics, and 2) determine if there is an episodic effect of decreased alkalinity and pH in the lakes following iceout. Because weather fronts move from west to east across Washington, it was assumed that most of the differences in acidity and ionic composition of snow collected in the Olympics and Cascades would be due to additions from the Seattle-Tacoma, urban-industrial area to the largely natural composition originating over the ocean.

Methods and Materials

Six cores were collected, three at each of two sites, one in the Cascade and one in the Olympic Mountains, during the spring of 1982. Cores were collected with a clean, anodized aluminum, standard core (4.1 cm diameter) from the Minotaur Lake basin (1700 m elevation) in the Cascades, 11 km north of Stevens Pass, and from the Morganroth Lake basin (1258 m elevation) in the Olympics (Fig. 1). These basins were selected for their high elevations and ease of access by helicopter.

Because mechanized equipment was not allowed in the wilderness area, it was necessary to locate the snow coring site in the Cascades where access was allowed, and at a similar high elevation and as near as possible to the Alpine Lakes Wilderness area lakes where lake chemical content was monitored. The Minotaur Lake basin lies only 30 km northeast of the sampled lakes (Fig. 1), and since most storms move across the Cascades from the southwest (Vong and Waggoner 1983), the deposition of acid in the Minotaur Lake basin would be expected to be rather similar to that near the sampled lakes.

Snow core depth ranged from 3.7 to 7.0 m at the Cascade site on 19 March 1982 and 2.7 to 4.9 m at the Olympic site on 1 April 1982. At each site, cores were collected from the lake surface, on the shore and about 50 m from the lake shore in a meadow area. The deepest snow cover was on the meadow at both sites.

Cores from the Cascades were melted and analyzed for major cations and anions in addition to pH and specific conductance. Samples for alkalinity, pH, and specific conductance were analyzed within a day or two after returning to the laboratory. Cores from the Olympic site were split to determine if a concentration effect had occurred in the lower half of the snow pack through the thawing-freezing process, which is prevalent

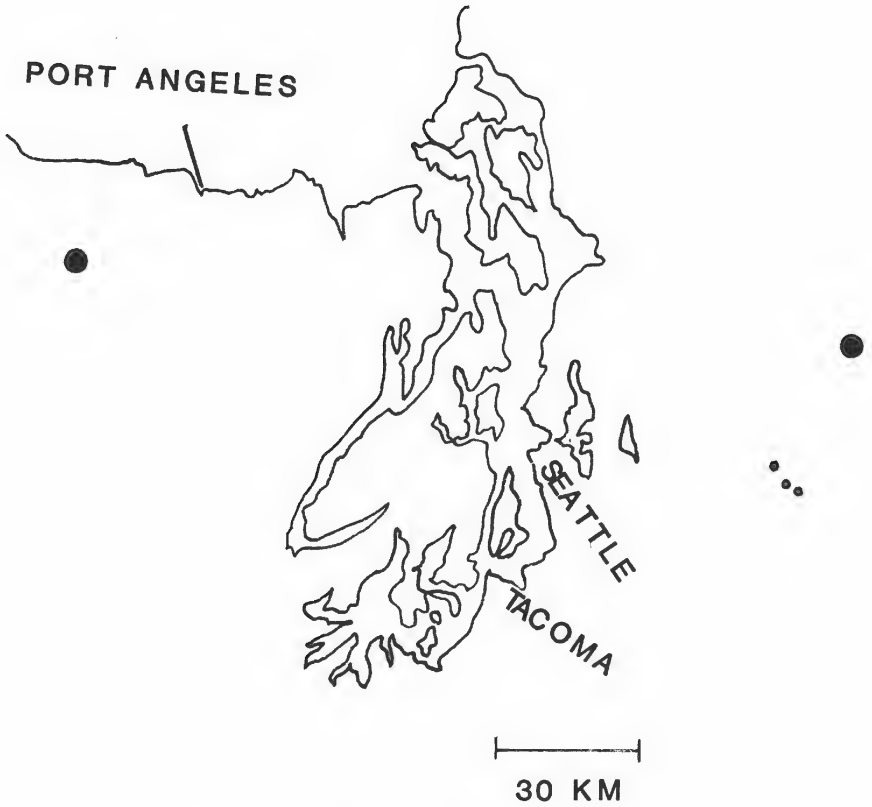

Figure 1. Western Washington showing the locations of alpine lakes (small circles) and snow core sites (large circles).

in Washington's mountain areas. There was no difference detectable in the constituents, so results are reported on the composite cores.

The anions, chloride, sulfate, and nitrate were determined by an ion chromatograph using a Dionex 3 x 500 mm standard anion exchange suppressor column. Bicarbonate was determined by alkalinity titration using the conductometric method (Golterman 1969, pp. 32 and 141). Precision for sulfate and chloride was $\pm$ 10 percent and $\pm$ 25 percent for nitrate. The alkalinity titration was prices to about $\pm$ 5 percent. The cations sodium calcium, magnesium, and potassium were determined with an Instrumentation Laboratory model 353 atomic absorption unit with a precision of about $\pm$ 10 percent. An Extech model 609 digital meter was used to determine pH using a dilute buffer. Comparison of the pH of snowmelt and lake samples determined in the field with two Extech meters ($n=11$) showed a mean deviation of $\pm$ 0.05 pH units, while comparison with two bench scale meters in the laboratory ($n=7$) showed a mean deviation of $\pm$ 0.12 units. Specific conductance was determined at 24 $\pm$ 0.5°C with a Barnstead model PM 70 meter.

Lake Samples

Samples were collected on three occasions in Big Heart Lake (1386m) and Copper Lake (1208 m); 23 July, 11 August, 24 August 1982. Angeline Lake was sampled on 23 July and 24 August. Samples were collected from a rubber raft at depths of 0, 5, 10, 20, and 50 m in each lake. Prior to filling, each bottle had been acid washed and throroughly rinsed and was rinsed again thoroughly with lake water. The bottles were filled completely and capped. An additional five samples, one from each depth, were collected for subsequent pH determination on shore.

The constituents determined and associated methods were the same as those used for snow. Alkalinity was also determined by the Gran method on some samples (Gran 1952). Results were essentially the same as with the conductometric method, mean $\pm$ SD for five replicates of a test sample were 101 $\pm$ 3.7 and 101 $\pm$ 1.4 μeq l^{-1} for the Gran and conductometric methods, respectively. The change in the slope of specific conductance with added acid proved to be a very precise and relatively rapid determination of alkalinity in those poorly buffered waters. As noted earlier, the precision at such low alkalinities (<100 μeq l^{-1}) is at least $\pm$ 5 percent.

TABLE 1. Ionic content of snow cores collected at three sites on and near Minotaur Lake in the Cascade Mountains and Morganroth Lake in the Olympic Mountains, Washington, on March 19 and April 1, 1982, respectively. Values are in μeq l^{-1}.

Lake and Location	pH	H^+	NH_4^+	Na^+	Ca^{++}	Mg^{++}	K^+	$SO_4^=$	NO_3^-	Cl^-	HCO_3^-	$\Sigma+$	$\Sigma-$
Minotaur L. (CASCADES)													
Lake Surface	5.2	6.3	3.5	19.2	23.9	5.7	6.9	16.0	5.5	20.6	20.1	65.5	62.2
Shoreline	5.4	4.0	6.0	23.6	30.4	5.0	10.2	12.6	11.2	20.7	26.2	80.6	70.7
Meadow	5.4	4.0	7.0	12.3	15.1	2.6	5.6	6.4	5.2	16.8	20.7	46.6	49.1
Morganroth (OLYMPICS)													
Lake Surface	5.6	2.5	4.7	15.6	7.7	3.1	4.6	3.8	1.1	10.0	17.3	28.2	33.1
Shoreline	5.5	3.2	3.8	13.7	12.4	2.6	2.0	6.4	0.93	11.7	16.9	37.7	35.9
Meadow	5.4	4.0	7.1	13.1	3.0	5.1	3.8	3.0	0.62	10.6	17.2	36.1	31.5

Snow Cores

Results from the cores are shown in Table 1. The differences in pH among all cores are only slight and within the error of determination. However, the sulfate content in the three Cascade cores was about three fold greater than that in cores from the Olympics. Nitrate, on the other hand, was eight fold greater in the Cascade snow. Calcium in the Cascade cores was substantially higher than in those from the Olympics (about 15 μeq l^{-1}), which could have been responsible for buffering against a lower pH in Cascade snow in spite of more nitrate and sulfate.

The mean values for sulfate and nitrate in the Cascade cores (respectively 11.7 and 7.3 μeq l^{-1}) are similar to six-month means in bulk precipitation collections at Snoqualmie pass reported by Logan *et al.* (1982). They found mean concentrations of 14.8 and 8.6 μeq l^{-1} for sulfate and nitrate, respectively.

The charge balance showed reasonably good accounting of the ions. The average cation:anion ratios for the Cascade and Olympic cores, respectively, were 1.05 and 1.12.

Nevertheless, Liljestrand and Morgan (1979) have found that the calculated pH from the charge balance can be in error by nearly $\pm$ 0.5 units.

TABLE 2. Alkalinity, specific conductance and pH determined at five depths in the top 50 m of three lakes in the Alpine Lakes Wilderness Area, Washington, during 1982.

	pH						Conductivity			Alkalinity		
	7/23		8/11		8/24		μmhos cm^{-1}			μeq l^{-1}		
Lake	Field	Lab	Field	Lab	Field	Lab	7/13	8/11	8/24	7/12	8/11	8/24
ANGELINE												
Surface	6.4	5.9	—	—	5.8	5.9	8.7	—	4.4	26.7	—	16.7
5 m	6.5	5.9	—	—	5.8	5.9	7.2	—	4.3	24.0	—	16.6
10 m	6.4	5.8	—	—	5.7	5.8	5.2	—	3.9	25.1	—	16.8
20 m	6.3	5.9	—	—	5.9	5.9	4.9	—	3.9	17.3	—	17.1
50 m	6.3	5.9	—	—	5.8	5.8	5.1	—	4.9	19.7	—	19.3
BIG HEART												
Surface	6.4	5.9	6.3	5.8	6.0	6.0	5.9	5.6	5.0	23.4	22.0	24.0
5 m	5.6	5.9	6.3	6.0	6.0	5.9	7.2	8.0	5.0	33.3	21.7	25.3
10 m	6.2	6.0	6.2	5.9	5.9	5.9	5.3	5.2	4.5	30.0	29.7	30.3
20 m	6.2	5.7	6.3	5.8	6.0	5.9	9.1	7.6	4.3	10.1	17.9	24.3
50 m	6.2	6.0	6.2	5.9	5.9	6.0	6.6	5.0	4.5	30.4	38.1	37.3
COPPER												
Surface	6.2	6.4	6.2	6.3	6.6	6.5	11.0	10.9	8.9	70.4	70.9	62.1
5 m	6.3	6.5	6.5	6.5	6.6	6.5	13.3	14.7	8.2	68.4	69.7	71.8
10 m	6.4	6.6	6.6	6.4	6.6	6.4	14.3	12.9	11.0	88.3	89.7	92.7
20 m	6.3	6.6	6.5	6.5	6.6	6.6	18.1	19.7	14.1	126.7	151.7	160.1
50 m	6.5	6.6	6.6	6.7	6.4	6.5	33.5	25.9	26.9	300.4	329.7	336.7

Lake Quality

Results from sampling the three lakes at three different times during the summer following iceout are shown in Table 2. Minimum pH was about 5.8, which occurred in Angeline Lake about a month after iceout. Values were slightly higher in Big Heart and 0.5 to 0.6 higher in Copper Lake. Field determinations of pH in Angeline and Big Heart gave higher values than laboratory determinations by about 0.2 to 0.5 units, except for the last samples. The agreement between field and laboratory measurements was good for Copper Lake. Alkalinity and specific conductance, as well, were higher in Copper than the other two lakes. Cation-anion balances for the three lakes are shown in Figure 2.

A consistent seasonal trend in alkalinity and pH was not apparent in any lake, although specific conductance values were lower in the three lakes at all depths in late summer compared to those observed earlier right after iceout. The means of the five depth samples (Table 2) changed during the summer from 6.2 to 4.3 umhos cm^{-1} in Angeline, from 6.8 to 6.3 to 4.7 in Big Heart, and from 18.0 to 16.8 to 13.8 in Copper. Except at Copper, there was no stratification of the concentration with depth.

An exception to this lack of trend in alkalinity and pH during the summer was in Angeline, where alkalinity in the upper 10 m did decrease with time, and an anomalously low alkalinity occurred at 20 m in Big Heart in the earliest samples. Overall, however, alkalinity values determined in the upper 10 m (six values in Angeline and nine each in Big Heart and Copper) varied rather consistently in the three lakes with means and standard deviations of 21.0 $\pm$ 4.8, 26.6 $\pm$ 4.2, and 76.0 $\mp$ 11.1 μeq l^{-1} for Angeline,

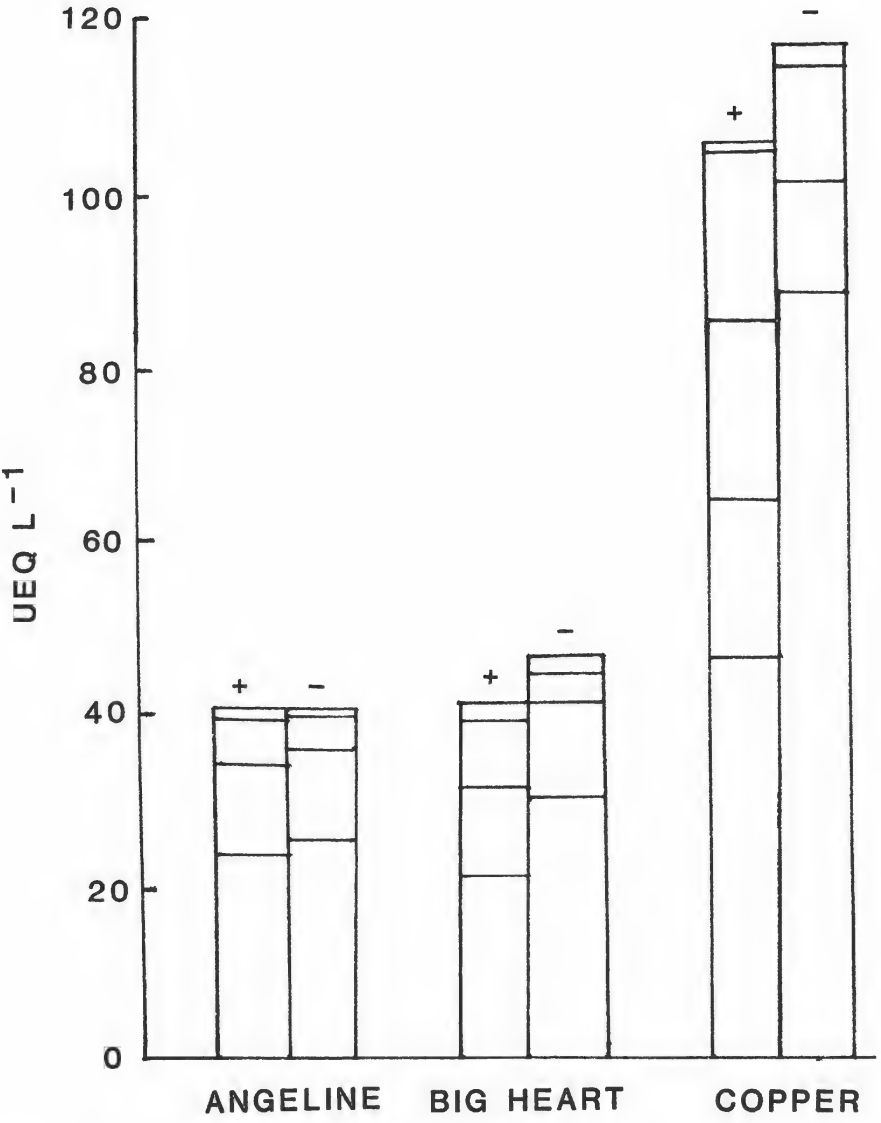

Figure 2. Cation-anion balance for three Alpine Lakes Wilderness Area lakes, 23 July 1982. Ascending order: cations—Ca, Na, Mg, K, H; anions—HCO_3, SO_4, Cl, NO_3.

Big Heart, and Copper, respectively; this is an average deviation of 18 percent. Considering that the analytical precision is $\pm$ 5 percent, an expected inlake/sampling variability in the surface waters may be about $\pm$ 13 percent.

Chemical stratification was pronounced in the upper 50 m in Copper Lake, but this was not the case in Angeline and was less apparent in Big Heart, the two higher eleva-

tion lakes. Figure 3 shows mean bicarbonate content with depth in the three lakes. Concentrations at depth in Copper Lake were consistently three to four times greater than those in the upper 10 m. Concentrations were rather uniform in Angeline, but except for the consistently lower values at 20 m, alkalinity tended to increase with depth in Big Heart, showing a greater tendency for stratification as in Copper. The lakes are all deeper than the sampled 50 m; Copper, Big Heart, and Angline, respectively, have maximum depths of 104, 168, and 155 m (Dethier *et al.* 1979).

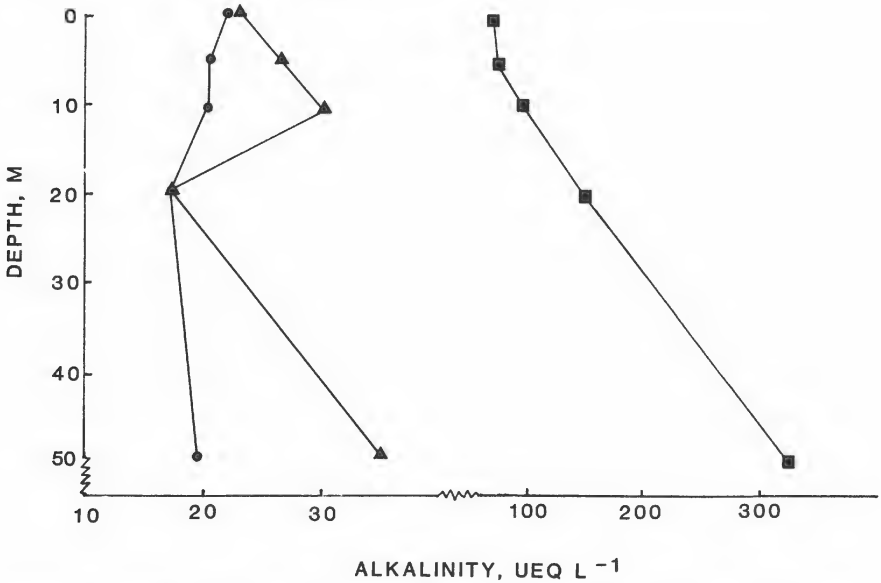

Figure 3. Distribution of alkalinity (HCO_3) with depth in the upper 50 m of Angeline (circles), Big Heart (triangles) and Copper (squares) Lakes during the summer of 1982. Values are means of two samples in Angeline and three each from Big Heart and Copper.

Discussion

Deposition of sulfate and nitrate appears to be greater in the Cascades downwind of the Seattle-Tacoma, urban-industrial area, than in the Olympics. Admittedly, this indication is based on only one set of three cores from one site in each area. However, the mean concentrations of sulfate and nitrate from the Cascade cores were similar, although 21 and 15 percent lower, than mean six-month values reported in precipitation from Snoqualmie Pass in 1981 by Logan *et al.* (1982). Their six-month mean sulfate concentration of 14.8 ueq l^{-1} from January through July, 1981, indicates that the rate of sulfate deposition was about 15 kg ha^{-1} during that period. About 10 percent of the strong acid content was due to nitrate and 60 percent to non-marine sulfate. Their mean precipitation pH was 4.7 while that from 1982 snow cores was 5.3. This comparison of the 1981 precipitation results of Logan *et al.*, with the snow content from 1982, is not entirely valid because Mount Saint Helens was still discharging significant amounts of sulfur dioxide in 1981, which no doubt had subsided more by the time the 1982 snow cores were collected.

Water sampling followed iceout in three lakes in the Alpine Lakes Wilderness area, about 30 km southwest of and at a similar elevation as the snow core site, did not reveal an episode of low pH and low alkalinity. The minimum pH observed, determined under laboratory conditions, was 5.8. Values were about 0.5 units higher in the lower elevation lake. It is not clear why field determinations on the first two occasions were 0.2 to 0.5 pH units higher than those measured in the laboratory. However, strong peaks in photosynthesis were observed to occur following iceout in another high Cascade lake (Hendrey and Welch 1974). Even modest photosynthetic rates could significantly raise pH in such poorly buffered waters. The discrepancy between field and laboratory pH determinations was in fact greater after iceout than later in the summer, which tends to support this hypothesis.

Considering that the pH of the snow may have been near 5.3, it was not surprising that a definite iceout episode did not occur. If the pH in the snow pack had been as low as the mean precipitation pH determined by Logan *et al.* at Snoqualmie Pass (4.7), a low pH episodic effect probably would have occurred, at least in the surface waters of these lakes. Except for ammonium, all cations were considerably higher in the Cascade snow cores than in the Snoqualmie Pass precipitation collected by Logan *et al.* This was especially true for calcium. There appears to have been some additional buffering in the snow pack with cations, as indicated from the cores, that was not found in precipitation reported by Logan *et al.* However, cores were collected in open areas in a lake basin with little vegetation and, therefore, should have represented precipitation only. Another possibility is that snow in the Cascades may not represent the most acidic precipitation falling on those high lake watersheds. Recent precipitation sampling at a lower elevation (180 m) west of the Alpine Lakes Wilderness area lakes shows that the annual mean pH was 4.6, but during spring and summer it was much more acid at pH 4.15 (Vong and Waggoner 1983).

Although acidity of the snowpack was not sufficient to cause an episode, the more dilute waters entering the surface waters of the lakes following iceout apparently produced some chemical stratification. This phenomenon was indicated in all three lakes by specific conductance, which decreased consistently over the one-month period. Dilution of the surface waters producing chemical stratification was most apparent in Copper, the lowest elevation lake sampled, where bicarbonate in the upper 10 m was one-fourth to one-third the bicarbonate content of the deeper water. There was a more subtle indication of this phenomenon in Big Heart, the next higher lake, but in Angeline, the highest in elevation, bicarbonate was relatively constant with depth and was similar to levels determined in the snowpack. The surface content of bicarbonate in Copper was only about two tenths that at 50 m; the ratio for specific conductance was one third. Stratification may exist at greater depths in the higher lakes also; nevertheless, lake alkalinity seems to be more affected by other sources of alkalinity (probably groundwater and weathering), as elevation decreases, than only the contents of snowmelt water.

This pattern of chemical changes due to snowmelt being restricted to the surface waters of lakes is probably typical of relatively deep lakes with low watershed area: lake area ratios. The two higher elevation lakes, which are over 150 m in depth, have watershed:lake surface ratios of about 5, and flushing rates crudely estimated at around 0.1 yr^{-1}. In such systems it can be assumed that the snowmelt water will move largely through the surface waters, even before iceout, as the constituent profiles in these lakes

may suggest. Hendrey *et al.* (1980) observed that snowmelt water in two Adirondack lakes with relatively small watershed : lake surface ratios (6.9 and 9.0), lowered the pH in the upper 1 m only, while the lake with a large ratio (69) became well mixed. The latter lake was deeper, but its flushing rate was 5.6 yr^{-1}, about threefold greater than the other two lakes.

In such systems that remain stratified during the snowmelt episode there would tend to be a refuge for mobile animals, such as fish, in the deeper waters, which would be relatively unaffected by the lowered pH of the snowmelt water. In shallower lakes with higher watershed:lake surface area ratios and consequent faster flushing rates, such stratification may not persist and there would be no refuge. Lakes with the latter morphometric and hydrologic characteristics would tend to be more sensitive biologically.

Acknowledgments

The research described in this article has been funded wholly by the United States Environmental Protection Agency through order agreement no. 2B0629NAEX to Eugene B. Welch; however, it has not been subjected to Agency review and therefore does not necessarily reflect the views of the Agency and no official endorsement should be inferred.

Literature Cited

Casadevall, P. J. et al. 1981. SO_2 emission rates at Mount St. Helens from March 29 through December 1980. *In* P. W. Lipman and D. R. Mullineaux, the 1980 eruption of Mount Saint Helens, Washington. U.S. Geological Survey Professional paper No. 1250, pp. 193-200.

Charlson, R. J., and H. Rodhe. 1982. Factors controlling the acidity of natural rainwater. Nature 295: 683-685.

Dethier, D. P. 1979. Atmospheric contributions to stream water chemistry in the North Cascade Range, Washington. Water Res. Research 15: 787-794.

———, P. L. Heller, and A. S. Safioles. 1979. Reconnaissance data on lakes in the Alpine Lakes Wilderness Area, Washington. U.S. Geological Survey, Open-File Report 79-1465.

Golterman, H. L. 1969. Methods for Chemical Analysis of Fresh Waters. IBP Handbook No. 8, Blackwell Scientific Publ. Oxford and Edinbourgh.

Gran, G. 1952. Determination of the equivalence point in potentiometric titrations. Part 2. Analyst, 77: 661-671.

Hendrey, G. R., and E. B. Welch. 1974. Phytoplankton productivity in Findley Lake. Hydrobiologia, 45: 45-63.

———, J. N. Galloway, and C. L. Schofield. 1980. Temporal and spatial trends in the chemistry of acidified lakes under ice cover. *In* D. Drablos and A. Tollan, eds. Int. Conf. Ecol. Impact Acid Precip., SNSF Proj. Rep., Norway, pp. 68-74.

Logan, R. M. 1980. Acid Precipitation at a Site on Stampede Pass, Washington. MS Thesis, Central Washington State University, Ellensburg.

———, J. C. Derby, and L. C. Duncan. 1982. Acid precipitation and lake susceptibility in the Central Washington Cascades. Environ. Sci. Technol, 16: 771-775.

Liljestrand, H. M., and J. J. Morgan. 1979. Error analysis applied to indirect methods for precipitation acidity. Tellus, 31: 421-431.

Omernik, J. M., and C. F. Powers. 1982. Total alkalinity of surface waters—a national map. EPA-600/D-82-333.

Powers, C. F. and D. L. Rambo. 1981. The occurrence of acid precipitation on the west coast of the United States. Environ. Monitoring and Assessment, 1: 93-105.

Vong, R. J., and A. P. Waggoner. 1983. The chemical composition of Western Washington rainwater. Project report to Environmental Protection Agency Region X, Department of Civil Engineering, University of Washington, 54 pp. (with appendices).

Wasem, R. 1982. Recent characteristics of precipitation pH in the Northern Cascade range. Presentation, Symposium on Acid Precipitation and Atmospheric Deposition: A Western Perspective, Bellingham, Wash.

Received April 13, 1983
Accepted for publication July 3, 1983

W. C. Mahaney

Department of Geography
Atkinson College
York University
4700 Keele Street
Downsview, Ontario M3J 2R7

Indian Basin Advance in Western and North-Central Wyoming

Abstract

Three Neoglacial fluctuations are recognized in the mountains of north-central and western Wyoming. The two youngest advances, Gannett Peak (300-100 yr BP) and Audubon (2000-1000 yr BP), are recognized and differentiated on the basis of vegetation and percent of lichen cover, weathering features, and soil development. The name Audubon advance was originally intended for use only in Colorado, but subsequent investigations over the last decade have shown that stratigraphic units of similar description and age are located in the Big Horn, Wind River, and Teton ranges. Because the name Temple Lake has been used for both pre- and post-Altithermal deposits, it is suggested that early Neoglacial deposits (5000?-3000 yr BP) be renamed from a type locality in the northern Wind River Range, Wyoming. After careful scrutiny of several high-altitude areas in the three ranges, Indian Basin was selected as a type locality. In this basin, a series of three end moraines and a medial moraine of early Neoglacial age are found below the Harrower Glacier. Descriptions of the weathering features, lichen characteristics, and soil morphology are used to place these deposits in the Holocene stratigraphic column.

Introduction

Following the Altithermal Interval of Antevs (1948), Neoglaciation led to the renewal of glacial activity in western North America. In the mountains of western and north-central Wyoming three advances during the Neoglacial are recognized. The younger deposits of Gannett Peak and Audubon advances have been mapped and described over much of western Wyoming (Mahaney 1974, 1978; Mahaney *et al.* 1981). Numerous deposits of early Neoglacial (formerly Temple Lake) age have been recognized in several cirques in three ranges. A type locality for these deposits is found in Indian Basin at 3300 m in the Wind River Range (Fig. 1), where the early Neoglacial record is well displayed and exposed. Three distinct sets of end moraines and a medial moraine located downvalley from the Harrower Glacier (Fig. 2) provide a setting in which weathering features, lichen characteristics, and soil morphology can be used to provide a diagnostic body of stratigraphic information. The type locality is used to introduce a new stratigraphic name—Indian Basin advance.

Previous Work

The name Temple Lake was used originally by Moss (1951) to refer to moraines equivalent in age to what eventually became known as Pinedale. Later Richmond (1960, 1962, 1965a, 1965b) used the term Temple Lake to encompass deposits laid down in the early Neoglacial. Benedict (1967, 1968) in the Colorado Front Range used radiocarbon dates, boulder weathering, and lichenometry to provide ages of 5000 to 3000 yr BP for deposits then believed equivalent in age. Because of the age controversy associated with the name Temple Lake, Benedict (1973) renamed early Neoglacial deposits using

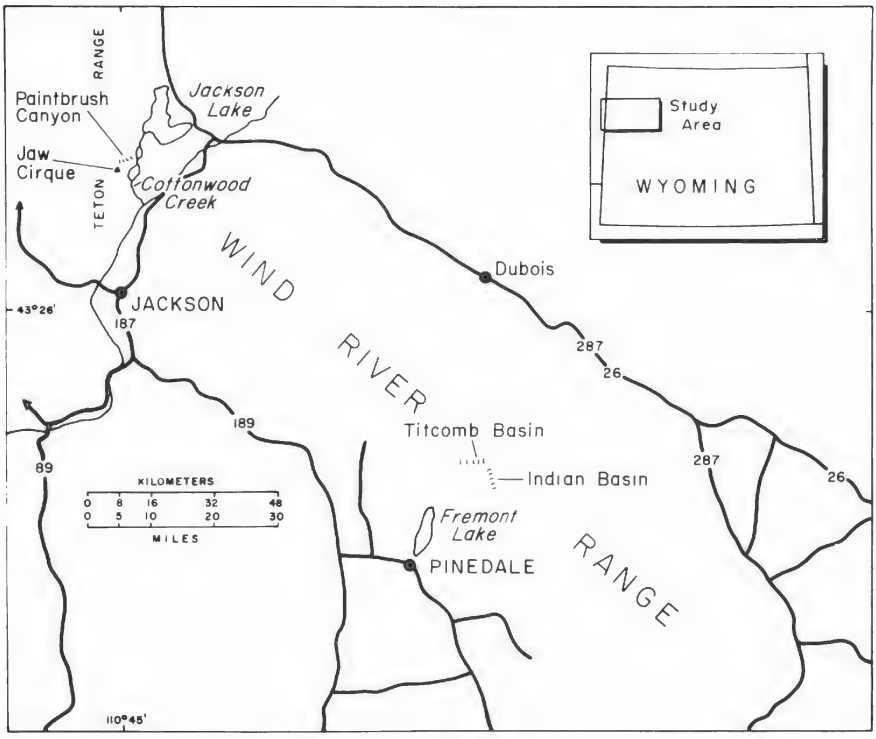

Figure 1. The Wind River Range.

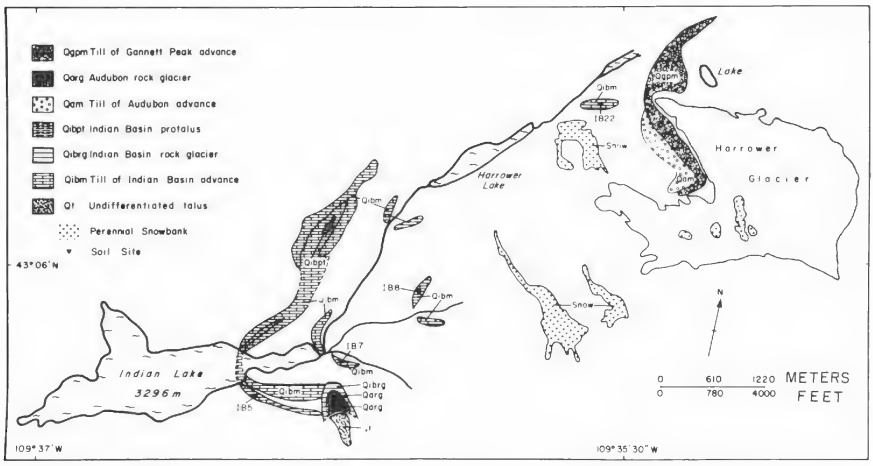

Figure 2. Three distinct sets of end moraines and a medial moraine located downvalley from the Harrower Glacier.

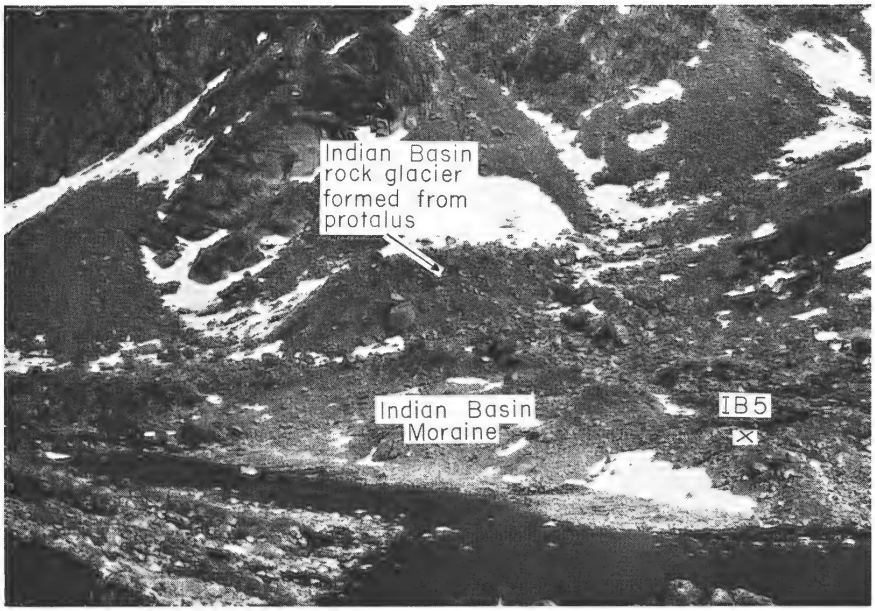

Figure 3. The proposed type area for Indian Basin deposits is located in the valley below Harrower Glacier near Indian Lake.

a Colorado name, Triple Lakes. Recent evidence suggests that some deposits believed to be equivalent in age to the Triple Lakes of Benedict may in fact predate the Neoglacial (Birkeland and Shroba 1974, Meierding and Birkeland 1980).

In Wyoming, the name Temple Lake was retained for early Neoglacial moraines, but the type locality was moved upvalley (south of Temple Lake) (Currey 1974.) At the same time, Miller and Birkeland (1974) pointed out that, "Changing a name or a locality will not solve all the problems," but in this case, retention of the name probably added to the controversy. Following my field work in Temple Cirque (1972), I concluded that the early Neoglacial record at that locality was relatively insignificant, and certainly not representative of other high altitude basins in the Wind River Range. Therefore, I referred to mid-Holocene glacial deposits as early Neoglacial (Mahaney 1975, 1978, 1981). Numerous mapping projects, weathering studies, lichenometric surveys, and soil-profile investigations (Mahaney 1978, 1981; Mahaney *et al.* 1983) showed that early Neoglacial deposits are present in most north-central and western Wyoming cirques, making it advisable to designate with minimum ambiguity the earliest of the Neoglacial advances.

After mapping and collecting samples in three ranges—including Temple Lake (Mahaney *et al.* 1983), Mammoth Basin, Stroud Basin, Titcomb Basin (Mahaney 1978, 1981), and Indian Basin (Mahaney *et al.* 1983) in the Wind River Range; Garnet, Cascade, Jaw, and Paintbrush canyons (Mahaney *et al.* 1981) in the Teton Range; and Cloud Peak Area in the Big Horn Mountains—I suggest that the name Indian Basin be used for early Neoglacial deposits. This decision is made after consultation with the

U.S. Geological Survey Names Committee (M. E. MacLachlan, pers. comm., 1982). The Code of Stratigraphic Nomenclature (A.C.S.N. 1970) contains no guidelines for the use of post-depositional modification such as weathering features, lichen characteristics, and soil morphologies in defining rock-stratigraphic units. Hence, the name Indian Basin is used informally to refer to any early Neoglacial advances that deposited material defined as such by physical characteristics resulting from postdepositional modification (Birkeland *et al.* 1979).

Type Area

The proposed type area for Indian Basin deposits is located in the valley below Harrower Glacier near Indian Lake (Figs. 2 and 3). These deposits have weathering, lichenometric, and soil morphologic features well representative of early Neoglacial deposits recognized in other areas. This is an important area to study because of the proximity of these deposits to younger late Holocene and older early Holocene (late Pinedale) deposits (Figs. 4 and 5), where relative weathering features and soil differences are apparent.

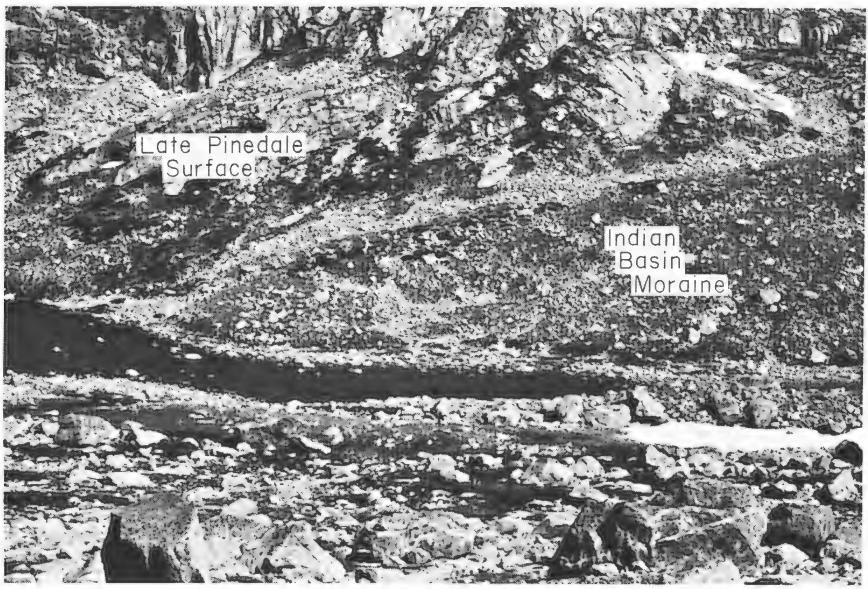

Figure 4. The Indian Basin Moraine and the Late Pinedale Surface.

Weathering Features and Lichenometry

Weathering characteristics, including ratio of fresh to weathered stones weathering rind thickness, and weathering pit depth and width, show that deposits of Indian Basin age are clearly older than deposits of Audubon age and are younger than late Pinedale deposits. The ratio of fresh to weathered stones is not useful in distinguishing between Neoglacial deposits; however, it is useful in separating Neoglacial deposits from older substrates of late Pinedale age (Mahaney 1978, Mahaney *et al.* 1983). In

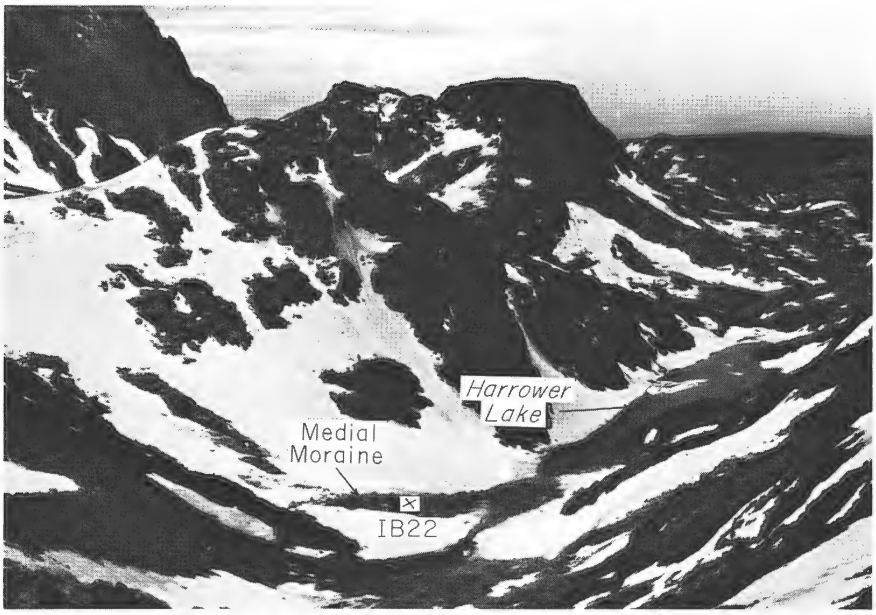

Figure 5. Harrower Lake and the Medial Moraine.

most instances, late Pinedale deposits have ratios of 1 to 3 percent weathered to 99 to 97 percent fresh stones, whereas Neoglacial deposits have 100 percent fresh stones. This observation suggests that weathering ratios are useful age indicators, but not sensitive enough to allow separation of deposits within a glaciation.

Weathering rind development on surface stones is highly variable and produces maximum and minimum thicknesses that vary between deposits of different age. While the maximum rind thickens with age, giving means ($n = 50$ and $n = 100$; Table 1) of 2.1 to 3.6 mm, the minimum rind is nil on Indian Basin deposits. Late Pinedale surface stones, on the other hand, have mean maximum rind thickness of +5.0 mm and mean minima are greater than nil (see Mahaney 1978, 1982; and Mahaney *et al.* 1983).

Weathering pit characteristics change with age of the substrate, and they are useful in distinguishing Indian Basin deposits from younger and older units in the geologic succession. For further discussion of the use of this data in age assignment see Mahaney *et al.* 1983.

Maximum lichen diameters and percent cover for the four dominant crustose lichens —*Rhizocarpon geographicum*, *Lecanora thomsonii*, *Lecanora aspicilia*, and *Lecidea atrobrunnea*—are used to distinguish between deposits in the Neoglacial stratigraphic succession. Lichen on surfaces of late Pinedale age are beyond the range of lichenometry. The data in Table 1 are useful in distinguishing among Neoglacial advances (*e.g.*, Gannett Peak, Audubon, and Indian Basin). Among the above four dominant crustose lichens, *R. geographicum* and *L. thomsonii* are the most significant because their maximum diameters fall into three discrete groups. *Lecidea aspicilia*, although absent on the youngest deposits of Gannett Peak age, occurs on older substrates. *Lecidea atrobrunnea*, absent

TABLE 1. Weathering characteristics[a], lichen thalli diameters, and percent lichen cover for sites on Figure 2, Indian Basin, northern Wind River Range, Wyoming.

Site[b]	Weathering Rinds Max	Min	n	R. geographicum	L. thomsonii	L. aspicilia	L. atrobrunnea	% Cover
IB5[c]	2.1	nil	50	72	110	148	118	50+
IB7	3.6	nil	100	85	98	140	121	50+
IB8	3.0	nil	50	70	101	160	96	30-50+
IB22	2.8	nil	50	39	106	151	105	15-80

[a]Measurements in millimeters
[b]For location see Figure 2
[c]Samples taken from B horizon in soil pit

on deposits of Gannett Peak age, appears on Audubon and Indian Basin deposits. Most significantly, percent of lichen cover, ranging from nil on Gannett Peak deposits to 15-30 percent on Audubon deposits, increases to more than 50 percent on Indian Basin surfaces.

Soils

Differentiation of Neoglacial deposits is further supported by soil morphological and clay mineralogical data. I have described and sampled 28 soil profiles of early Neoglacial age forming in topographically high and well-drained sites, in the alpine vegetation and climatic zones, and in materials consisting largely of till with clasts of granite and granodiorite. The IB5 soil profile (Table 2) is representative of early Neoglacial profiles sampled in the Wind River, Teton, and Big Horn ranges.

TABLE 2. Soil profile[a] IB5 in Indian Basin, Wind River Range.

Horizon	Depth (cm)	Description
01	1-0	Black (10YR 1.7/1; 2/1)
A1	0-7	Grayish yellow brown (10YR 4/1m), and dull yellowish brown (10YR 5/3d) sandy loam, granular structure, friable moist consistence, slightly plastic and non-sticky.
IIB	7-20	Dull yellowish brown (10YR 5/4m), brown (10YR 4/4m), and dull yellow orange (10YR 7/3d) pebbly sandy clay loam, weak blocky structure, friable moist consistence, nonplastic and slightly sticky.
IICox	20-69	Dull yellowish brown (10 4/3m, 5/3m) yellowish brown (2.5Y 5/3m), and dull yellow orange (10YR 7/2d) pebbly sandy loam, massive, friable moist consistence, nonplastic and nonsticky.
IICn	69+	Dark olive (5Y 4/3m) and light gray (2.5Y 8/2d) pebbly sandy clay loam, massive, friable to very friable moist consistence, nonplastic and nonsticky.

[a]Soil descriptions follow Soil Survey Staff (1951) and Birkeland (1974); soil colors are from the standard Soil Color Charts of Oyama and Takehara (1967) and are given in the moist (m) and dry (d) states.

The post-Indian Basin soil, an Inceptisol tentatively classified as a Dystric Cryocrept according to criteria of the Soil Survey Staff (1975) is representative of early Neoglacial soils studied in several high-altitude basins. This soil contains clear and distinct horizon

contacts to a depth of 69 cm. Horizon identity rests on color changes, with soil showing 10YR and the parent material 2.5Y hues. Sandy and sandy clay loam textures dominate throughout the profile, with high percentage of pebbles and cobbles in the lower solum and subsoil. Textures become finer with depth in the profile as clay increases downward, possibly a result of illuviation (Table 3). Granular structure in the A1 horizon

TABLE 3. Particle-size distributions for the soil horizons in the >2mm and <2mm fractions of four post-Indian Basin profiles, type area, northern Wind River Mountains, Wyoming.

Site	Horizon[b]	Depth (cm)	Location[a]	Pebbles %	Sand-Silt-Clay %	Sand % (2mm-63μm)	Silt % (63-4μm)	Clay % (<4μm)
IB5	A1	0-7	Outer	15.5	84.5	53.6	25.9	20.5
	IIB	7-20	End	26.8	73.2	61.4	14.6	24.0
	IICox	20-69	Moraine	25.3	74.7	62.3	15.2	22.5
	IICn	69+		33.2	66.8	62.5	14.0	23.5
IB7	A1	0-8	Intermediate	19.3	80.7	53.3	30.7	16.0
	IIB	8-20	End	32.4	67.6	68.1	25.4	6.5
	IIC1ox	20-53	Moraine	44.3	55.7	65.1	23.9	11.0
	IIC2ox	53-72		42.5	57.5	67.8	21.7	10.5
	IICn	72+		39.3	60.7	65.3	22.7	12.0
IB8	A1	0-9	Inner	9.9	90.1	33.3	35.7	31.0
	B	9-28	End Moraine	30.7	69.3	35.9	36.6	27.5
	IIC1ox	28-55		68.9	31.1	78.8	14.2	7.0
	IIC2ox	55-83		70.4	29.6	83.4	12.9	3.7
	IICn	83+		31.5	68.5	78.2	17.0	4.8
IB22	A1	0-6	Medial	23.9	76.1	63.4	23.6	13.0
	B	6-18	Moraine	23.5	76.5	53.8	32.7	13.5
	Cox	18-80		54.0	46.0	62.7	30.5	6.8
	IICn	80+		50.7	49.3	70.0	17.0	13.0

[a]For location see Figure 2.
[b]Till/loess boundary (II/I) determined by high silt in the solum or subsoil.

and a weak grade of blocky structure in the B horizon are characteristic of post-Indian Basin soils (Mahaney 1982). Oxidation effects deduced from soil hues (10 YR 4/4m in the B horizon) suggest some chemical weathering.

Mineral material finer than 2mm is dominantly sand in most cases (Table 3). In all profiles there is an upward fining sequence of silt, suggesting airfall influx of material. In most instances, the high silt layer forms a cap on the soil profile; however, in profile IB22 it appears to be a mechanical mix of loess and till to a depth of 80 cm. Clay ($<4\mu$m) is generally highest in the sola of the three soils, presumably the result of weathering *in situ* and aeolian influx. However, in profile IB5 clay increases somewhat in the lower solum, and overall it is fairly uniformly distributed with depth.

Mineralogical analysis of the clay grade size ($<2\mu$m) was carried out by X-ray diffraction, following procedures outlined by Whittig (1965). The results in Table 4 show little variation within the primary mineral suites. However, lower quartz and feldspar in the solum of IB8 may be the result of weathering since the middle phase of early Neoglaciation. Differences in clay mineral composition show that illite, which is highest in the parent materials (Cn horizons), decreases or disappears altogether in the soil sola where smectite and illite-smectite tend to increase. However, in the IB8 profile smectite and illite-smectite are abundant in the subsoil and parent material. Over-

TABLE 4. X-ray analysis of the <2μm fraction of four post-Indian Basin soils, type area, northern Wind River Mountains, Wyoming.

Site	Horizon	Depth (cm)	K	H	I	S	I-S	V	C	Q	P
IB5	A1	0-7	tr	—	—	—	—	tr	—	xxx	x
	IIB	7-20	xx	?	x	xx	xx	—	x	xxx	x
	IICox	20-60	x	tr	x	x	x	—	x	xxx	x
	IICn	69+	x	tr	x	x	x	—	x	xx	x
IB7	A1	0-8	xxx	xx	x	xxx	xxx	xx	xx	xxx	xxx
	IIB	8-20	xxx	xx	x	xxx	xxx	xx	xx	xxx	xxx
	IIC1ox	20-53	xxx	xx	xxx	xx	xxx	xxx	xx	xxx	xx
	IIC2ox	53-72	—	x	xxx	—	xxx	xxx	xx	xxx	xxx
	IICn	72+	—	tr	xx	—	xxx	xx	x	xxx	xxx
IB8	A1	0-9	—	—	tr	tr	x	x	x	x	x
	IIB	9-28	—	tr	—	tr	tr	tr	tr	—	x
	IIC1ox	28-55	xx	tr	—	xxx	xxx	xxx	xx	xxx	xxx
	IIC2ox	55-83	xxx	tr	x	xxx	xxx	xxx	xxx	xxx	xxx
	IICn	83+	xxx	?	x	xxx	xxx	xx	xxx	xxx	xx
IB22	A1	0-6	?	—	—	?	tr	—	—	xxx	xx
	B	6-18	tr	—	x	xx	xx	x	x	xxx	xx
	Cox	18-80	tr	—	x	tr	x	—	—	xxx	xx
	IICn	80+	tr	—	xxx	x	x	—	x	xxx	xx

[a]Minerals are kaolinite (K), halloysite (H), illite (I), smectite (S), illite-smectite (I-S), vermiculite (V), chlorite (C), quartz (Q), plagioclase feldspar (P). Mineral amounts are given semi-quantitatively as nil (—), minor amount (tr), small (x),, moderate (xx), and abundant (xxx).

all, the relative increase of smectite in the B and C horizons of post-Indian Basin profiles (relative to the parent materials) is part of a general pattern observed in other soil chronosequences in the Wind River Range. On the other hand, post-Indian Basin soils in the Teton Range have little smectite, a characteristic attributed to the parent material, which is composed largely of felsic gneiss and granite.

Conclusions

The data discussed herein are intended to provide a corpus of stratigraphic information to be used to recognize deposits of Indian Basin age in the mountains of western Wyoming. These deposits have weathering, lichenometric and soil morphologic features that are diagnostic of early Neoglacial deposits recognized in many high altitude valleys of the Teton, Wind River, and Big Horn ranges. While weathering criteria allow separation of Indian Basin substrates from older late Pinedale deposits, the most important relative dating methods for subdividing deposits within the Neoglacial include lichen characteristics and the degree of soil development. An important characteristic of post-Indian Basin soils is that they often contain moderate to large amounts of smectite and illite-smectite, apparently the result of weathering from illitic-rich parent materials.

Literature Cited

Amer. Comm. Strat. Nomen. 1970. Code of stratigraphic Nomenclature, Amer. Assoc. Petrol. Geol.

Antevs, E. 1948. Climatic changes and pre-White man, *in* The Great Basin, with Emphasis on Glacial and Post-glacial Times, Univ. of Utah Bull. 38: 168-191.

Benedict, J. B. 1967. Recent glacial history of an alpine area in the Colorado Front Range, U.S.A. Establishing a lichen-growth curve. Journal of Glaciology 6: 817-832.

———. 1968. Recent glacial history of an alpine area in the Colorado Front Range, U.S.A. II. Dating the glacial deposits. Journal of Glaciology 7: 77-87.

———. 1973. Chronology of Cirque glaciation, Colorado Front Range. Quaternary Research 3: 584-599.
Birkeland, P. W. 1974. Pedology, Weathering and Geomorphological Research. N.Y., Oxford.
———, S. M. Colman, R. M. Burke, R. R. Shroba, and T. C.Meierding. 1979. Nomenclature of alpine deposits, or What's in a name. Geology 7: 532-536.
——— and R. R. Shroba. 1974. The status of the concept of Quaternary soil-forming intervals in the western U.S. *in* W. C. Mahaney (ed.), Quaternary Environments: Proc. of a Symposium, Geographical Monographs 4: 241-276.
Currey, D. R. 1974. Probable pre-Neoglacial age of the type Temple Lake Moraine, Wyoming. Arctic and Alpine Research 6: 293-300.
Mahaney, W. C. 1975. Soils of post-Audubon age, Teton Glacier Area, Wyo.: Arctic and Alpine Research, v. 7 No. 2: 141-154.
———. 1978. Late-Quaternary stratigraphy and soils in the Wind River Mountains, western Wyoming, *in* W. C. Mahaney (ed.) Quaternary Soils, Norwich, U.K. Geoabstracts Ltd.: 223-264.
———. 1981. Paleoclimate reconstructed from paleosols: evidence from the Rocky Mountains and East Africa, *in* W. C. Mahaney (ed.), Quaternary Paleoclimate, Geoabstracts, Norwich, U.K.: 227-247.
———, D. Halvorson, J. Piegat, and K. Sanmugadas. 1983. Evaluation of dating methods used to assign ages to Quaternary deposits in the Wind River and Teton Ranges, western Wyoming, *in* W. C. Mahaney (ed.), Quaternary Dating Methods: Stroudsburg, Pa., A. M. Dowden Publishers, 335-374.
Meierding, T. C. and P. W. Birkeland. 1980. Quaternary glaciation of Colorado, *in* H. C. Kent and K. W. Porter (eds.), Colorado Geology, Rocky Mountain Assoc. of Geol.: 165-173.
Miller, C. D. and P. W. Birkeland. 1974. Probable pre-Neoglacial age of the type Temple Lake Moraine, Wyoming: Discussion and additional relative-age data. Arctic and Alpine Research 5, 6: 301-306.
Moss, J. H. 1951. Late Glacial advances in the Southern Wind River Mountains, Wyo. Am. Jour. Sci 249: 865-883.
Oyama, M. and H. Takehara. 1967. Standard Soil Color Charts.
Richmond, G. M. 1960. Glaciation of the east slope of Rocky Mountain National Park, Colorado, Bull. Geol. Soc. Am., v. 71 (9): 1371-1382.
———. 1962. Quaternary statigraphy of the La Sal Mountains, Utah. U. S. Geol. Surv. Prof. Pap. 324: 135.
———. 1965a. Type moraines of the Pinedale Glaciation, *in* C. B. Schultz and H. T. U. Smith (eds.), Guidebook for Field Conference E: Lincoln, Nebr., Nebr. Acad. Sci. Ser. VII, INQUA Congr.: 34-36.
———. 1965b. Glaciation of the Rocky Mountains, *in* H. E. Wright, Jr. and D. G. Frey (eds.), The Quaternary of the United States. Princeton, N.J., Princeton University Press: 217-300.
Soil Survey Staff. 1951. Soil Survey Manual, Washington, U.S. Govt. Printing Office.
———. 1975. Soil Taxonomy, Washington, U.S. Govt. Printing Office.
Whittig, L. D. 1965. X-ray techniques for mineral identification and mineralogical composition, *in* C. A. Black (ed.), Methods of Soil Analysis. Amer. Soc. Agron., Madison, Wisc.: 671-696.

Received July 6, 1983
Accepted for publication October 18, 1983

Crystal J. Driver

and

Ronald J. Kendall

Huxley College of Environmental Studies
Western Washington University
Bellingham, Washington 98225

Lead Shot Ingestion in Waterfowl in Washington State, 1978-1979

Abstract

A total of 762 waterfowl gizzards was collected from Washington State during the 1978-79 hunting season. Lead shot were present in 33 (4.3 percent) of the gizzards of 10 species of waterfowl represented. Only gizzards of Pintails (*Anas acuta*) and Mallards (*Anas platyrhynchos*) contained lead pellets. The incidence of lead shot ingestion in Mallards was 4.6 percent statewide. Mallards collected from western Washington had lead shot present in 4.1 prcent of gizzards as compared to 0.5 percent in gizzards of Mallards from eastern Washington.

Introduction

Ingestion of spent lead shot has been recognized as an important cause of waterfowl mortality since 1874 (Phillips and Lincoln 1930). More than 6000 tons of lead shot are expended into waterfowl feeding areas by hunters every year (Montague and Montague 1973). Consequently, ducks and geese ingesting lead shot in all four major flyways across the United States have been affected by lead poisoning (Grinnell 1901, Wetmore 1919, Mohler 1954, and Trainer and Hunt 1965). Bellrose (1959) estimated that plumbism accounted for the mortality of 2 to 3 percent of the total fall population of waterfowl in North America. Incidence of lead poisoning along the Pacific Flyway has been estimated to be 4.9 percent, or about twice the national average (Bellrose 1959).

Nearshore bottom sediments of waterfowl feeding areas in Washington State may contain up to a reported 34,000 lead pellets per hectare (34/sq. meter) in the state's lakes and marshes (Adkins 1975). Waterfowl appear to be at risk of ingestion of spent lead shot in Washington State. However, recent studies by the Washington State Department of Game suggest a decline in statewide lead shot ingestion by waterfowl. Ingestion rates dropped from 5.3 percent for the 1973-74 hunting season to 4.5 percent in 1976-77. In the 1977-78 season, the incidence of lead shot in waterfowl gizzards was 2.6 percent (Henry 1979). Because lead poisoning in waterfowl has occurred in hunting areas, steel shot regulations for waterfowl have been adopted. The present study was undertaken to assess the occurrence of lead and steel shot in gizzards of waterfowl in the State of Washington during the 1978-79 hunting season.

Methods

Gizzards of hunter-killed waterfowl were collected at public hunting areas broken down on a county basis in the State of Washington during the 1978-79 hunting season. In

addition, Gray's Marsh, a private hunting reserve in Clallam County, contributed 108 Mallard gizzards to the study.

Specimens were received by Washington State Department of Game field personnel and frozen in plastic bags until examined in our laboratory. Gizzards were opened and contents examined for lead pellets by the hydraulic method developed by Brewer (1981). Shot were identified as lead, steel, or copper. Penetrated gizzards were identified, and any shot present was examined for erosion under a dissecting microscope. If erosion of the pellet was apparent, it was assumed to have been ingested.

Results

A total of 762 waterfowl gizzards was collected from 11 counties in Washington State during the 1978-79 hunting season. Lead shot were present in 33 (4.3 percent) of the gizzards (Table 1). One copper shot was found in a Mallard (*Anas platyrhyncos*) from

TABLE 1. Incidence of lead and copper shot in gizzards of waterfowl from Washington State, 1978-1979.

Species	No. of Gizzards	% of Waterfowl Collected	No. of Gizzards with Lead Shot	% of Species with Lead Shot Present in Gizzard	% of Total Sample with Lead Shot
Mallard (**Anas platyrhynchos**)	565	74.3	26	4.6	3.4
Pintail (**Anas acuta**)	70	9.2	4	5.7	0.5
Gadwall (**Anas strepera**)	2	0.3	0	—	—
American Widgeon (**Mareca americana**)	29	3.8	0	—	—
G. W. Teal (**Anas carolinensis**)	14	1.8	0	—	—
Redhead (**Aythya americana**)	2	0.3	0	—	—
Canvasback (**Aythya valisineria**)	6	0.8	0	—	—
Scaup (**Aythya affinis**)	3	0.4	0	—	—
Total Duck	698	91.6	30	10.3	3.9
Canada Goose (**Branta canadensis**)	74	9.7	2	2.6	0.3
Brant (**Branta nigricans**)	4	0.5	1	25.0	0.1
Total Goose	85	11.2	3	3.5	0.4
Total Waterfowl	762		33		4.3

the Corfu Reserve in Grant County (Table 2). No steel shot was present in any of the gizzards. Of those waterfowl gizzards that contained lead shot, 70 percent had 1 pellet (Table 3). Only gizzards from Mallards contained more than 2 lead shot per gizzard, except for 2 Pintails (*Anas acuta*) that had 4 and 8 shots in their gizzard (Table 3).

Of the eight species of ducks collected, only gizzards from Mallards and Pintails contained lead pellets. The incidence of lead shot ingestion in Mallards for the 1978-79 season was 4.6 percent statewide (Table 1). Eastern Washington Mallards showed low ingestion rates (0.5 percent) compared to Mallards from western counties (4.1 percent) (Table 4). The incidence of ingested lead shot in Pintails was 5.7 percent (Table 1). All Pintails that had ingested lead shot were collected from the Willapa Refuge in Pacific County (Table 4).

Three of 85 (3.5 percent) goose gizzards contained lead pellets (Table 1). Two

TABLE 2. Sample distribution and incidence of lead shot in waterfowl gizzards collected from 12 Washington counties, 1978-1979.

County	No. of Gizzards	% of Waterfowl Collected	No. of with Lead Shot Gizzards	% of All Waterfowl Collected from Each County with Lead Shot in Gizzard	% of Total
Adams	146	19.2	3	2.1	0.4
Franklin	11	1.4	0	—	—
Grant	235	30.8	2*	0.9	0.3
Lincoln	63	8.3	0	—	—
Yakima	2	0.3	0	—	—
Columbia	2	0.3	0	—	—
East	459	60.3	5	—	—
Whatcom	101	13.3	1	1.0	0.1
Skagit	5	0.7	1	20.0	0.1
King	2	0.3	0	—	—
Clallum	108	14.2	20	18.5	2.6
Pacific	87	11.4	7	8.1	0.9
West	303	39.9	29	—	3.7
Total	762	100	34	—	4.4

*Includes one copper shot.

TABLE 3. Frequency distribution of numbers of ingested shot per gizzard for waterfowl collected in Washington State during the 1978-1979 hunting season.

Species	No. of Gizzards with Lead Shot	1	2	3	4	8
Mallard	26	18	3	4	1	0
Pintail	4	2	0	0	1	1
Canada Goose	2	2	0	0	0	0
Brant	1	1	0	0	0	0
Total	33	23	3	4	2	1
Percent	(100)	(69.7)	(9.1)	(12.1)	(6.1)	(3.0)

TABLE 4. Lead shot incidence in waterfowl from hunting areas where lead shot were ingested.

Species	County (Refuge)	No. of Gizzards (%)	No. of Gizzards with Lead Shot Present (%)
Mallard		565	
	Grant (Wanapum)*	200 (35.4)	1 (0.5)
	Adams (Othello)*	88 (15.6)	2 (2.3)
	Whatcom (Hampton Lake)+	83 (14.7)	1 (1.2)
	Clallum (Grays March)+	108 (19.1)	20 (18.5)
	Pacific (Willapa)+	13 (2.3)	2 (15.4)
Pintail		70	
	Pacific (Willapa)	34 (48.6)	4 (11.8)
Canada Goose		74	
	Adams (Othello)	32 (43.2)	1 (3.1)
	Pacific (Willapa)	14 (18.4)	1 (7.1)
Brant		4	
	Skagit	4 (0.5)	1 (25.0)

*Eastern counties in the State of Washington had 3 Mallard gizzards with lead shot present; 0.5 percent of total Mallard gizzards.

+Western counties in the State of Washington had 23 Mallard gizzards with lead shot present; 4.1 percent of total Mallard gizzards.

of the positive gizzards were collected in western Washington, although most samples were taken from the eastern counties.

Discussion

Previous studies have suggested a decline in lead shot ingestion by waterfowl collected from Washington State since the 1973-74 hunting season. Dropping from 5.3 percent in 1973-74, the statewide lead shot ingestion rate was 2.6 percent in waterfowl during the 1977-78 season (Henry 1979). In the present study, the lead shot incidence in waterfowl was found to be 4.3 percent (Table 1), with 60 percent of the gizzards coming from the eastern portion of the state (Table 2). Although the 4.3 percent ingestion rate tended to be higher than the 2.6 percent rate repored for the previous hunting season (Henry 1979), it compares closely with the mean (4.4 percent) ingestion rate over three seasons (Henry 1979). Bellrose (1959) reported that the incidence of lead shot ingestion in waterfowl in the Pacific Flyway was 4.9 percent.

As in previous seasons, the incidence of lead shot ingestion tended to be higher in the western portion of the state (3.7 percent) than in the eastern counties (0.7 percent) (Table 2). It should be noted that Clark County, the county having the highest statewide incidence of ingested lead and steel shot in waterfowl in 1977-78, was not sampled during the 1978-79 season. In eastern Washington, only two gizzards were from Yakima County, whereas over 200 were from this county in 1976-77 and in 1977-78. Therefore, conclusions from these data should be limited, although there appears to be a higher incidence of lead shot ingestion in waterfowl collected from the western part of the State of Washington.

The percentage of gizzards with lead shot that contained only one pellet was 69.7 percent. Bellrose (1959) earlier reported a similar figure of 65.5 percent from the Pacific Flyway. In 1973-74, the percentage of gizzards with lead shot that contained a single pellet was 92.8 percent declining to 64.6 percent in 1977-78 (Henry 1979). Bellrose (1959) described an inverse relationship between pellets per gizzard and ingestion rates for waterfowl species. Therefore, in Washington waterfowl, Henry (1979) suggested that the increase in the number of shot per gizzard from 1973 to 1977 reflects an upward trend in total ingestion rates. Since our data do not reflect a continued drop in the percentage of gizzards containing a single lead pellet, the total ingestion rate has possibly stabilized.

Acknowledgments

Waterfowl gizzards were provided by the Washington State Department of Game. Appreciation is extended to Mr. Larry Brewer for providing a hydraulic separation device for gizzard analyses.

Literature Cited

Adkins, J. 1975. Lead shot analysis—Skagit County. Status report on lead shot availability to waterfowl submitted to Washington State Department of Game. February 1975.

Bellrose, F. M. 1959. Lead poisoning as a major factor in waterfowl population, Illinois. Natural History Survey Bulletin, Vol. 27, Article 3.

Brewer, L. W. 1981. A new apparatus for separating lead shot from waterfowl gizzard contents. Journal of Wildlife Management 45:496-498.

Grinnell, G. C. 1901. American Duck Shooting. Forest and Stream Publishing Co., New York. 598-601.

Henry, P. M. 1979. A study of ingested shot in waterfowl taken during the 1973-74, 1976-77, and

1977-78 hunting seasons in Washington. Department of Game Management, Game Management Division.
Mohler, L. 1954. Lead poisoning of geese near Lincoln. Nebraska Bird Review 13:49-50.
Montague, P., and K. Montague. 1973. Getting the lead out—switch to steel shot takes decades. Audubon 75:115-117.
Phillips, J. C., and F. C. Lincoln. 1930. American Waterfowl: Their Present Situation and the Outlook for Their Future. Houghton Mifflin Company, Boston and New York.
Trainer, D. O., and R. A. Hunt. 1965. Lead poisoning of waterfowl in Wisconsin. Journal of Wildlife Management 29:96-103.
Wetmore, A. 1919. Lead poisoning in waterfowl. U.S.D.A. Bulletin 793:1-12.

Received May 21, 1982
Accepted for publication August 13, 1982

Roger Rosentreter

Department of Botany
University of Montana
Missoula, Montana 59812

The Zonation of Mosses and Lichens Along the Salmon River in Idaho

Abstract

Communities of mosses and lichens below high water mark on the Salmon River in Idaho are viewed as distinct associations. These zones may be as much as several meters in depth. Based on the species present and on fluctuating water levels, four zones are found. Results from paired transects indicate that stability of the substrate, force of the current, and distance above the low water level determine species dominance. Compared to the headwaters, the lower reaches of the river have more favorable conditions for growth of mosses and lichens and for development of zonation patterns.

The Salmon River is unique because it is the largest river in the western United States that does not have regulatory dams. Its headwaters are protected by Wilderness and Wild and Scenic River designations. The Salmon River originates in the granitic Idaho Batholith in central Idaho, and the lower section flows over basalt. The zonation described in this paper occurs on both granite and basalt along the course of the river.

Lichens and other forms of vegetation can be used for flood frequency analysis and for calculating river channel capacity (Gregory 1976). Lichens may also be useful in water quality studies (Hawksworth 1974). The zonation of plants along a river can be used for the prediction of discharge from channel geometry at ungauged sites (Gregory 1976). Furthermore, absence of lichens from suitable habitats may indicate river channel disturbance or modification.

Crytogam zonations along streams have been reported by Hale (1950), Glime (1970), Pentecost (1977), and Craw (1976). These zones were no broader than 10 cm per zone and less than 40 cm total (Craw 1976). In comparison, zonation along the Salmon River is higher and therefore more significant for use in management. Since the Salmon River fluctuates as much as several meters in depth, these broad zones may be useful indicators of flood frequency and flood levels (Fig. 1).

The purpose of this study is to describe the lichen and moss associations found along the Salmon River and to relate differences in species composition to hydraulic characteristics of the channel and to substrate stability. Also of interest is the way in which plant associations changed over the river's course.

Study Area

The study area included the Main and the Middle Fork of the Salmon River, Idaho, USA. The Middle Fork was studied from Dagger Falls (1767 m) downstream to its confluence with the North Fork of the Salmon. The main Salmon River was studied from its confluence with the Middle Fork to its mouth at the Snake River (335 m).

Spring snowmelt in the mountainous headwaters results in maximum flows, and

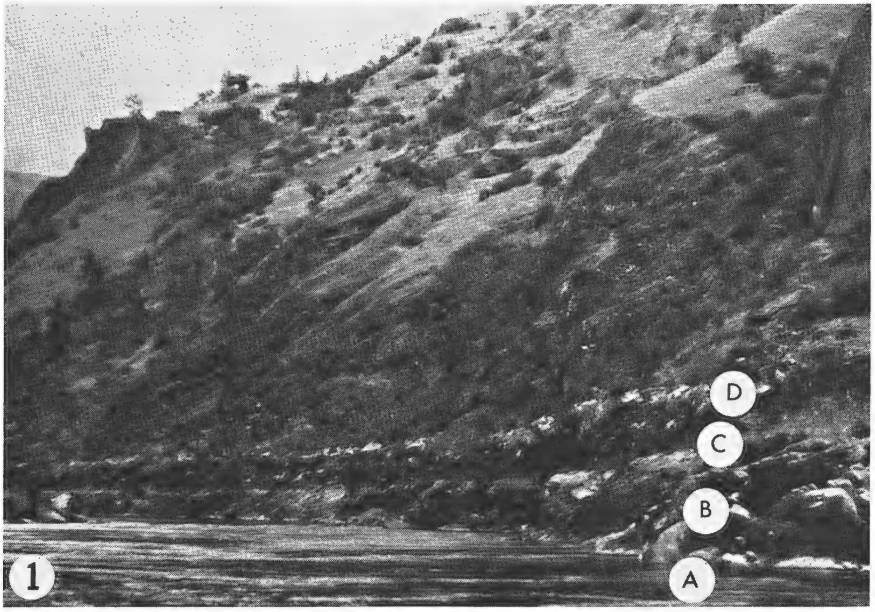

Figure 1. An overview of vegetation zones on the lower reaches of the Salmon River in Idaho: A. Low Water Zone; B. Normal Flood Zone; C. High Flood Zone; D. Extreme Flood Zone.

minimum flows occur in winter (December). Measurements for Whitebird, Idaho (lower main Salmon) are as follows: 64 year average discharge, 320 m^3/sec (11,290 cfs); maximum recorded discharge 3,680 m^3/sec (130,000 cfs) 17 June 1974; minimum recorded discharge, 44.7 m^3/sec (1,580 cfs) 11 December 1932 (U.S. Geological Survey 1976).

The topography of the study area varies from steep hills to a narrow canyon with vertical walls. The river channel is usually controlled by bedrock and thus is narrow and rarely meanders.

The surrounding vegetation varies from mesic forests in the upper reaches and on north-facing slopes to xeric grasslands in the lower reaches and on south-facing slopes. The forest habitat types are in the *Pseudotsuga menziesii* (Douglas fir) and *Pinus ponderosa* (Ponderosa pine) series (Steele *et al.* 1981). Shrub steppe communities occur on steep open slopes and rocky areas; these include *Artemisia, Purshia,* and *Cercocarpus. Amelanchier, Rhus, Alnus,* and *Populus* are the riparian shrubs and trees in the side draws and drainages. The grasslands have the potential to support *Agropyron spicatum* (Bluebunch wheatgrass) and *Festuca* (fescue) habitat type series (Tisdale 1979).

Methods

Sampling consisted of ten paired transects at intervals of approximately 70 km along the course of the river. Paired transects allowed comparison of species responses to

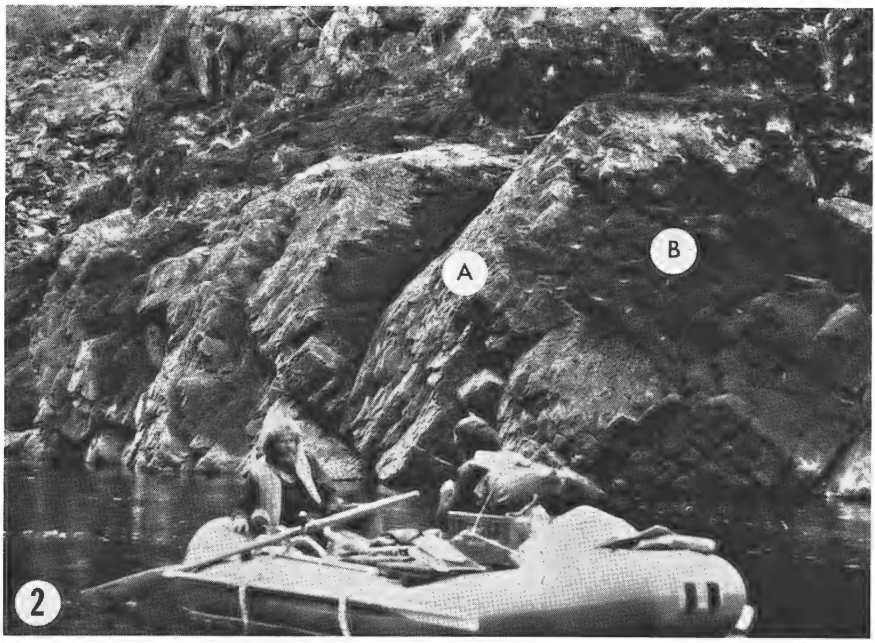

Figure 2. Effect of current force in the normal flood zone on the Salmon River in Idaho: A. The upstream side of the rocks which receive the stronger current are covered by *Dermatocarpon reticulatum*; B. The protected eddy side of the rocks are covered by *Scouleria aquatica.*

hydraulic conditions unaltered by elevation or by other changing environmental conditions along the river's length. At each site, individual transects were selected to include variation in stream hydraulic conditions. For example, a transect pair might have one transect in a direct current and a second transect at the same rapid on a similar rock type but in an eddy current. River rocks that were altered by man, with a known disturbance date, were noted but were not used for transect sites.

Sampling was done in a low water period, allowing easy access to seasonally flooded areas. Line transects ran perpendicular to the shoreline from water level through the high flood level, as marked by the occurrence of strictly terrestrial vegetation. For each decimeter point along the transect line, species presence was recorded. The intervals between points were narrow enough to detect such small-scale topographic changes as the top or side of a small boulder.

At each decimeter point on the transects, the following data were recorded: 1) location in the current, 2) rock type, 3) degree of siltation, 4) percent slope, and 5) species. Species that occurred in fewer than four transects are not reported here, nor are occasional vascular plants occurring beneath sample points. Instead, the nearest non-vascular species were recorded if they were present within 1 dm^2. Percent cover was calculated by species presence at sampled dm points over the total dm points in a transect.

Species of *Verrucaria* were not separated in the sampling. *Barbula rubiginosa* and

Grimmia montana are often difficult to destinguish in the field without sporophytes, and flood waters physically batter the leaf awns, so they were counted together in the transect data.

Nomenclature of lichens and mosses follows lists of Hale and Culberson (1970) and Crum *et al.* (1973). Nomenclature of vascular plants follows that of Hitchcock and Cronquist (1973). Voucher specimens for the cryptogams are at MONTU.

Photographs were taken at various sites along the river. Since these may be useful for comparison in further studies of the area, 18 of the photographs are on file at the Idaho Historical Society Library, Boise, Idaho.

Results and Discussion

The results from transect pairs placed in contrasting current forces indicate the importance of current to community composition (Fig. 2 and Table 1). As current force

TABLE 1. The average percent frequency (with 95% confidence interval) of species in the normal flood zone from 10 paired transects contrasting stream hydraulic conditions.

	Transects in Strong Current	Transects in Weak Current
Scouleria aquatica	9.7% ± 7.3	89.6% ± 9.5
Dermatocarpon reticulatum	28.7% ± 10.4	9.4% ± 9.6
Verrucaria spp.	40.0% ± 10.1	0.0% ± 0.0
Bare rock (no species present)	21.5% ± 14.2	1.2% ± 0.9

decreases, species dominance shifts from *Verrucaria* spp. to *Dermatocarpon reticulatum* and finally to *Scouleria aquatica.*

Several distinct zones of vegetation corresponding to recurrent flood patterns were found along the Salmon River: low water zone, normal flood zone, high flood zone, and extreme high flood zone. The characteristic species in each zone are as follows (Fig. 4):

1. Low water zone—*Verrucaria* spp. and algae.
2. Normal flood zone—*Dermatocarpon reticulatum* or *Scouleria aquatica.*
3. High flood zone—*Barbula rubiginosa* and *Grimmia montana.*
4. Extreme high flood zone—barren of vegetation or occupied by terrestrial vegetation.

For vascular plants associated with seasonal flooding along the Salmon River see Appendix A.

Irregular and recurrent disturbances are a part of many climax communities; for example, fires are a part of some climax Ponderosa pine communities (Steele *et al.* 1981). The moss and lichen zones are apparently adapted to and maintained by different flood frequencies and durations. These communities do not appear to be successional states leading to other vegetation types, nor do they accumulate soil. Two old photographs from the early 1900s (60-52.869 and 60-175.19 in the Idaho Historical Society Library) show the presence of these vegetational zones, proving their prolonged existence.

Zones on smooth vertical walls were distinct at a resolution of 1 dm. However, zones on broken topography did not have distinct divisions. These irregularities can be explained by physical configuration and are comparable to the vegetational zones

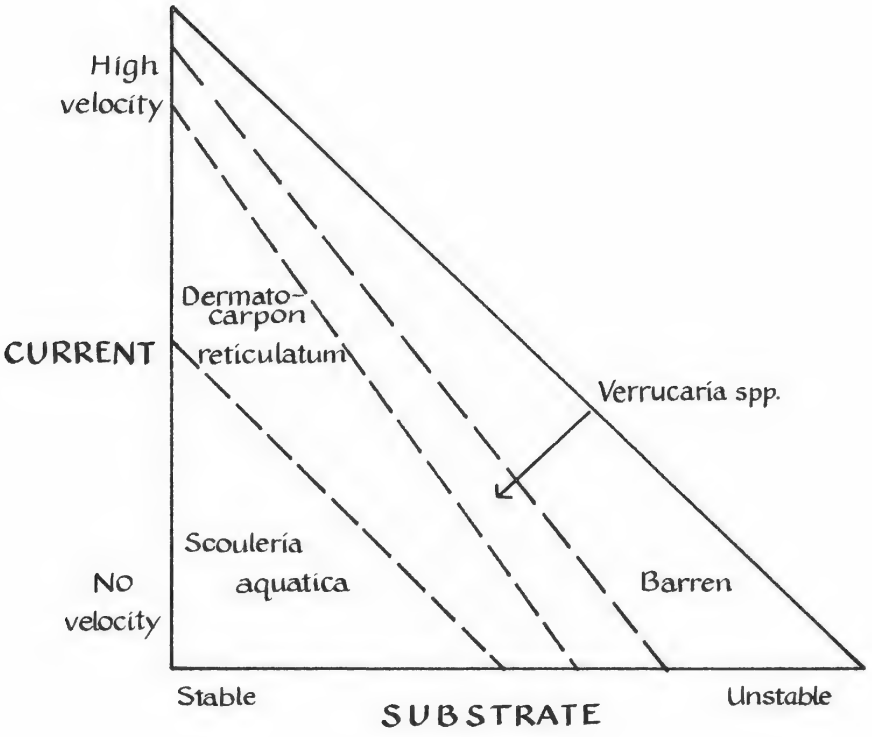

Figure 3. Hypothetical model for the effect of current velocity and substrate stability in controlling species composition in the normal flood zone.

found on a mountainside with broken topography. Sampling at decimeter intervals recorded irregularities that caused some noise in the zonation patterns; a larger sampling interval might avoid this. Nevertheless, what appears as noise in the results may be explained at a finer level of analysis as substrate stability, orientation of microsites to the current, and sheltering by other rocks.

Low Water Zone

The low water zone containing *Verrucaria* spp., crustose lichens, was poorly sampled in transects because much of the zone was submerged. *Verrucaria* is adapted to and occurs on submerged rocks in many regions of the world (Swinscow 1968).

Normal Flood Zone

The normal flow zone contained *Dermatocarpon reticulatum*, an umbilicate lichen, and *Scouleria aquatica*, a moss. Species dominance is apparently determined by substrate stability, current force, and height above the water level.

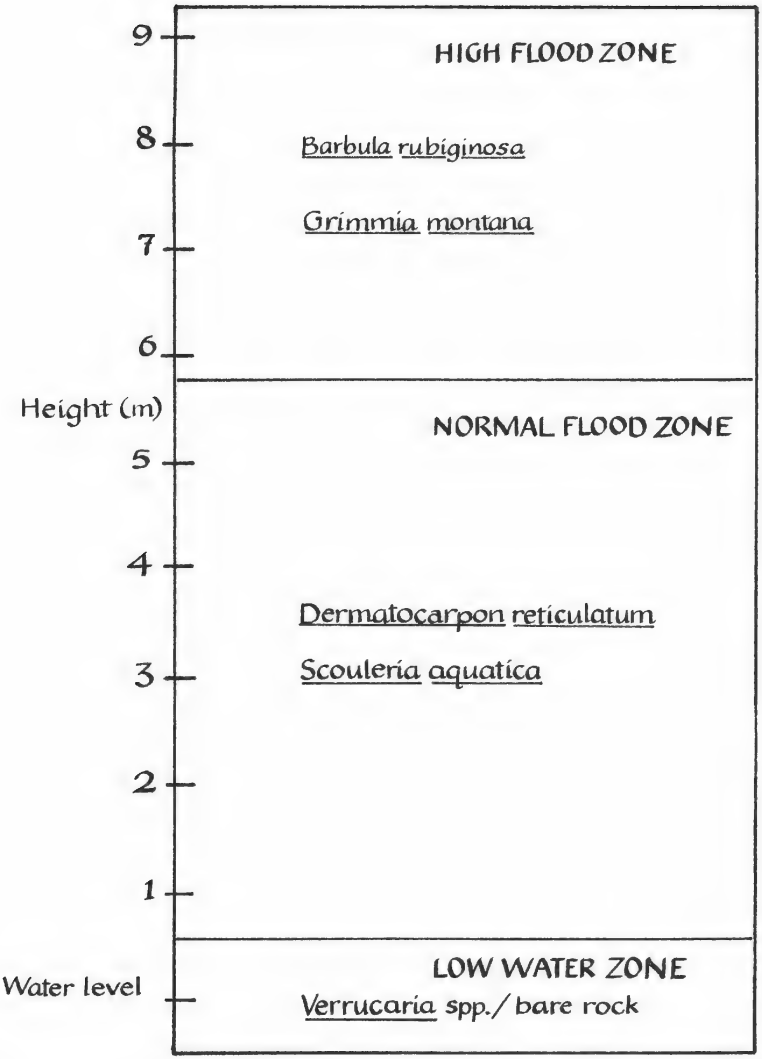

Figure 4. Species composition within zones and actual heights (± 1 dm) of each zone taken from the average of two eddy transects at Telcher Creek on the lower reaches of the Salmon River in Idaho.

Sites with increasingly stable substrate had a higher proportion of *S. aquatica,* less of *D. reticulatum,* and least of *Verrucaria* spp. (Fig. 3). Unstable substrates were often in the same location as strong current; in such cases the factors controlling the vegetation were not clearly distinguishable. An unstable substrate may be a soft, easily

eroded rock type (Swinscow 1968) or a hard rock type that moves as part of the bed load. River banks must contain stable rock material to support a moss or lichen flora ("a rolling stone gathers no moss"). Bed load formulae (Hebertson 1969, Einstein 1950) are based on the principle that the capacity of the stream to transport sediment along its bed varies directly with the difference between the shear stress acting on the bed particles and the critical shear stress required for initiation of particle motion. The bed load is related to the amount of water, the stream's profile, and the hydraulic gradient; therefore, the greater the bed load capacity, the larger the rock which can be transported (U.S. Bureau of Reclamation 1973).

Colonization by aquatic lichens is slow (Swinscow 1968). For example, large boulders (1 m^3), which were moved in 1930 for road construction, show no moss or lichen flora colonization now, although a rich flora is adjacent to the boulders.

Current velocity controls the vegetational distribution in several ways. Increased current velocity is directly related to an increased ability to carry greater suspended loads. The type, size, speed, and amount of the suspended load in a river appears to determine distribution of mosses and lichens in its channel. For example, the Grand Canyon of the Colorado River carries large amounts of course sand and silt in its suspended load and has no moss or lichen flora (personal observation), whereas a river such as the Salmon, with a moderate suspended load, can support an aquatic moss and lichen flora.

The structure of the river channel creates differences in current force and, in consequence, differences in species dominance. Results from the transect pairs indicate that, as current increased, the vegetation became structuraly more compact and tougher in texture. Transects located in stronger currents consistenly contained *D. reticulatum,* which has a more compact growth habit and is apparently tough-textured, rather than the soft-textured *S. aquatica* (Fig. 2 and Table 1). Compact growth habits were less susceptible to destruction by hydraulic pressure. The textural difference may reflect selection by the abrasive forces. The less abrasive the forces occurring at a site, the softer the texture of the species than can occupy these sites. Therefore, the force of current, size, speed, and amount of sediment load within a river's cross-section determines the species composition at any given site.

High Flood Zone

The high flood zone contained two mosses, *Barbula rubiginosa* and *Grimmia montana.* This zone occurs along the river's course more consistently than any other zone. Height above mean water level was the only factor that appeared to relate to the high flood zone. Given a long period without a high flood, terrestrial vegetation probably could temporarily invade this zone.

Extreme High Flood Zone

The extreme high flood zone is an area that usually supports terrestrial vegetation. In 1974, an extremely high flood occurred which clearly marks this zone (Fig. 1). At present, this zone is predominantly barren of vegetation. The aquatic mosses and lichens in the other three flood zones are strongly attached to the rock substrate. Therefore, these species resisted the destructive hydraulic and abrasive forces of the extreme high flood, whereas terrestrial species were dislodged. The age of terrestrial

species present in the extreme high flood zone could be used to date the occurrence of the last previous extreme high flood (Gregory 1976).

Patterns of presence and absence of vegetation suggest conditions required for the survival of aquatic moss and lichen communities. These requirements are a stable substrate, lack of strong abrasive forces, fluctuating water levels, and high dissolved carbon dioxide levels (Ruttner 1963, Gessner 1950).

The Salmon River is ideally suited for an aquatic moss and lichen flora zonation. Much of the stream channel is composed of solid stable bedrock or large stable boulders; the abrasive forces are moderate and decrease in areas not in the direct current; the Salmon is undammed and naturally exhibits a large recurrent seasonal fluctuation; and it is rapid throughout its length, which results in an abundant supply of dissolved carbon dioxide. Mosses are unable to photosynthesize using only bicarbonate ions as a carbon source (Ruttner 1963, Hynes 1970). Therefore, they are confined to water where there is an adequate supply of dissolved carbon dioxide. Rapids also protect streamside vegetation by restricting destructive winter ice floes to the midstream.

Comparison of Zonation between Headwaters and Lower Reaches

The headwaters had an average total height ($\pm$ 95 percent confidence interval) of streamside lichen and moss zones of 1.9 m ($\pm$ .3 m), compared to that of over 8.0 m ($\pm$ 1.1 m) for the lower reaches. Headwater transects had an average of only 80 percent ($\pm$ 32) cover compared to 99 percent ($\pm$ 2) cover in the lower reaches.

These differences may be explained as follows. First, the headwaters have a more open canyon topography with less stable rocks. The river gradient is steeper and thus the suspended load can be of a larger size and speed than in the lower reaches. Flooding of the headwaters is of short duration because of the small size and narrow elevational range of its drainage. By comparison, the lower reaches of the river drain a much larger area and a broader elevational range, resulting in more frequent floods of longer duration. The aquatic moss and lichen flora in the lower reaches is therefore consistentliy flooded for a longer period of time than those in the headwater reaches.

Since the climate is wetter in the upper reaches, there are more seepage areas that are not dependent on flooding for moisture. In comparison, the lack of moisture in the xeric climate of the lower reaches makes more of the flora dependent upon flooding. These differences may account in part for the greater development of zonation patterns in the lower reaches.

Information from this study could be used in several ways. The *Barbula*-high flood zone could be used as an indicator of channel capacity and of high flood level at unguaged sites. At any given site and date, the water level could be compared to the vegetational zones, thereby evaluating the flood state. The frequency of high flood that determines the *Barbula*-high flood zone could, in a future study, be calculated by correlating the *Barbula* level to flood levels at a gauged site. Species composition at any given site could tell us about the stability of that substrate and the force of the current at that site.

Acknowledgments

I thank Mason Hale of the Smithsonian Institution, Jack Stanford of the University of Montana Biological Station, and Bruce McCune for their comments on this paper.

Literature Cited

Craw, R. C. 1976. Streamside bryophyte zonations. New Zealand Journal of Botany 14: 19-28.

Crum, H. A., W. C. Steere, and L. E. Anderson. 1973. A new list of mosses of North America north of Mexico. The Bryologist 76: 85-130.

Einstein, H. A. 1950. The Bedload Functions for Sediment Transportation in Open Channel Flows. USDA Soil Conservation Service Technical Bulletin No. 1026.

Gessner, F. 1950. Die okologische Bedeutung der Stromungscheindigkeit Fliessender Gewasser und ihre Messung auf Kleinstem Raum. Archivs für Hydrobiologie 43: 159-165.

Glime, J. M. 1970. Zonation of bryophytes in the headwaters of a New Hampshire stream. Rhodora 72: 276-279.

Gregory, K. L. 1976. Lichens and determination of river channel capacity. Earth Surface Process 1: 273-285.

Hale, M. E. 1950. The lichens of Aton forest, Connecticut. The Bryologist 53: 181-213.

———, and W. L. Culberson. 1970. A fourth checklist of the lichens of the continental United States and Canada. The Bryologist 73: 499-543.

Hawksworth, D. L. 1979. Lichens and indicators of environmental changes. Environmental Change 6: 380-386.

Hebertson, J. G. 1969. A critical review of conventional bed load formulae. Journal of Hydrology 8: 1-26.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Hynes, H. B. N. 1970. The Ecology of Running Waters. University of Toronto Press, Toronto, Canada.

Pentecost, A. 1977. A comparison of two mountain streams in Gwynedd. Lichenologist 9: 107-111.

Ruttner, F. 1963. Fundamentals of Limnology. University of Toronto Press, Toronto, Canada (English transl.).

Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittams. 1981. Forest Habitat Types of Central Idaho. Intermountain Forest and Range Experiment Station Technical Report INT-114, Ogden, Utah.

Swinscow, T. D. V. 1968. Pyrenocarpus lichens: thirteen freshwater species of *Verrucaria* in the British Isles. Lichenologist 4: 34-54.

Tisdale, E. W. 1979. A Preliminary Classification of Snake River Canyon Grasslands in Idaho. Forest Wildlife and Range Experiment Station Notes No. 32, Moscow, Idaho.

United States Bureau of Reclamation. 1973. Design of Small Dams. A Water Resource Technical Publication, Second Edition.

United States Geological Survey. 1976. Water Resources Data for Idaho Water Year 1975. Water Data Report, ID-75, National Technical Information Service, Springfield, Virginia.

Appendix A

Vascular plants associated with seasonal flooding along the Salmon River.

Genus Species	Common Name	Common Site
Corydallis caseana	Corydalis	(headwaters only) silt
Dodecatheon jeffreyi	shooting star	(headwaters only) silt
Artemisia lindleyana	riverbank woodworm	rock or sandy areas
Aster hesperius	willow aster	rocky silted areas
Equisetum variegatum	variegated horsetail	water seeps (partial shade)
E. arvense	field horsetail	water seeps
E. hyemale	common horsetail	water seeps
Juncus spp.	rush	water seeps
Eleocharis spp.	spike-rush	standing water
Salix sp.	willow	variable
Carex nudata	torrent sedge	in silt
Elymus innovatus	riverbank wildrye	rocky silted areas
Mentha spp.	mint	variable
Rhus trilobata	poison ivy	disturbed and variable
Melilotus officinalis	yellow sweet clover	variable
Glycyrrhiza lepidota	licorice-root	(lower reaches) sand
Chrysopsis villosa	golden hairy aster	rounded river rocks
Tanacetum vulgaris	tansey	(lower reaches) deep silt
Conyza canadensis	horseweed	dry

Panicum scribnerianum	scribner witchgrass	water seeps
Bromus tectorum	cheatgrass	variable to dry sites
Chenopodium boytres	feather geranium	(lower reaches) sand
Apocynum androsaemifolium	dogbane	rocky, sand/silt areas
Celtis reticulata	hackberry	(lower reaches) variable
Zanthium strumarium	cocklebur	(lower reaches) sand

Received March 14, 1983
Accepted for publication June 25, 1983

David E. Pflug[1]

and

Gilbert B. Pauley

Washington Cooperative Fishery Research Unit[2]
College of Ocean and Fishery Sciences
University of Washington
Seattle, Washington 98195

Biology of Smallmouth Bass (Micropterus dolomieui) in Lake Sammamish, Washington[3]

Abstract

Smallmouth bass (*Micropterus dolomieui*) grew very rapidly in Lake Sammamish, with mean averages of 10.1 cm (1-year), 18.5 cm (2-year), 26.0 cm (3-year), 31.4 cm (4-year), 35.7 cm (5-year), 38.3 cm (6-year) and 41.4 cm 7-year). Most of the fish were 2- and 3-year-old bass, representing 39 and 24 percent of the total population respectively. Incremental growth was greatest between the ages of 1 and 3 and progressively decreased between the ages of 4 and 7. The growth rate exceeds that observed in most other North American waters. While crayfish (*Pasifastacus leniusculus*) and sculpins (*Cottus* sp.) made up a major part of the diet in most months, migratory salmon (*Oncorhynchus* sp.) were the most important prey item in the month of May, at the peak of the salmonid outmigration. Evidence is presented to support the theory that smallmouth bass do not selectively feed on salmon but are random feeders, eating whatever prey item is available. A regression line plot of prey length versus smallmouth bass size showed a positive correlation between prey size and predator size. The preferred habitat of the smallmouth bass was characterized by a hard substrate combined with a dropoff from an overbank and the absence of aquatic vegetation.

Introduction

Because of the growing interest in smallmouth bass (*Micropterus dolomieui*) by anglers in the state of Washington, a study was undertaken to learn more about the life history of this fish in a natural lake in Washington. Research concerning this important game fish in the Northwest has been confined to the Columbia and Snake Rivers and their associated tributaries (Henderson and Foster 1956, Keating 1970, Munther 1970, Montgomery *et al.* 1980).

Lake Sammamish has a thriving stock of smallmouth bass, as evidenced by the growing number of anglers each year on the lake, which is situated in an urban setting 16 km east of Seattle. Significant game fish populations of other species exist in the lake; these include resident trout (*Salmo* sp.) and anadromous salmon (*Oncorhynchus* sp.), most of which originate in the Issaquah Creek Salmon Hatchery at the South end of the lake. The lake is used as a transportation route for the massive outmigration of smolts from the hatchery each spring and the subsequent return of adult salmon to the hatchery

---

[1]Present Address: R. W. Beck & Associates, Tower Building Seventh and Olive Way, Seattle, Washington 98101.

[2]The Unit is jointly supported by the Washington State Department of Game, the Washington State Department of Fisheries, the University of Washington, and the U.S. Fish and Wildlife Service.

[3]Contribution Number 653, School of Fisheries, University of Washington, Seattle, Washington.

each fall (Pflug 1981). Since one of the major concerns in transplanting smallmouth bass into new waters is their potential impact on any resident trout or anadromous salmon populations, Lake Sammamish offers a unique setting for the study of smallmouth bass biology. The objectives of this study were to provide data on the following life history parameters: age and growth; spawning and nesting areas; habitat preference; food and feeding; and impact on existing salmon and trout populations in the lake. This paper describes these various aspects of the life history of smallmouth bass in Lake Sammamish, Washington.

Materials and Methods

For this study, Lake Sammamish was subdivided into 23 littoral sections of various sizes (Fig. 1). Sectional boundaries were established where visual changes occurred in the littoral habitat type, such as a depth profile transition, presence or absence of aquatic vegetation, and littoral substrate changes.

Shoreline habitat assessments, based on identifiable physical elements, were conducted on each section of the lake. Three distinct elements were used to make these sectional assessments: (1)littoral substrate type, (2) littoral depth profile, and (3) aquatic vegetation type and density. Four distinct substrates were identified: (1) silt, (2) sand, (3) gravel (6 to 40-mm diameter), and (4) cobble (40 to 250-mm diameter). Four littoral depth profile types were: (1) shallow flats—small depth change with increasing distance from shoreline; (2) gradual slope—moderate depth change with increasing distance from shoreline; (2) drop-off from overbank—moderate slope yielding to a steep drop-off; and (4) drop-off—steep drop starting directly from the shoreline. Aquatic vegetation densities were classified visually as dense, moderate, spotty, or absent (Goodpasture 1979).

Electrofishing and angling were the two methods used for collection of smallmouth bass in Lake Sammamish since these sampling techniques have been shown to be the most effective for securing large numbers of live bass (Bennett 1970). Electroshocking was conducted nocturnally and angling occurred diurnally between March and September of both 1979 and 1980. Additional samples of smallmouth bass were obtained from organized bass tournaments that were conducted during both sampling seasons.

During the 1979 and 1980 sampling seasons the following information and samples were optained from each of 734 smallmouth bass: (1) total length in centimeters, (2) weight in grams, (3) a scale sample taken near the base of the pectoral fin, and (4) the stomach contents extracted for identification. Corollary information taken from 695 fish (Table 3) included sections of capture and release, maturity, date, and method of capture.

Scales were soaked and cleaned in a water solution and non-regenerative scales were selected and mounted on strips of clear cellulose acetate with a heated vertical hydraulic press (Campbell and Witt 1953). The plastic slide impressions of the scales were viewed with a microfiche reader at 48× magnification. Age determinations were made by interpreting and counting the growth zones (annuli) that appeared on each non-regenerative scale. To determine the length of smallmouth bass at younger ages, the scale radius was measured between the mid-point of the focus and the outer margin, along the primary radii. A back calculation technique was used (June 1979), measuring the distance from the focus to each annulus on the sacle to estimate the corresponding

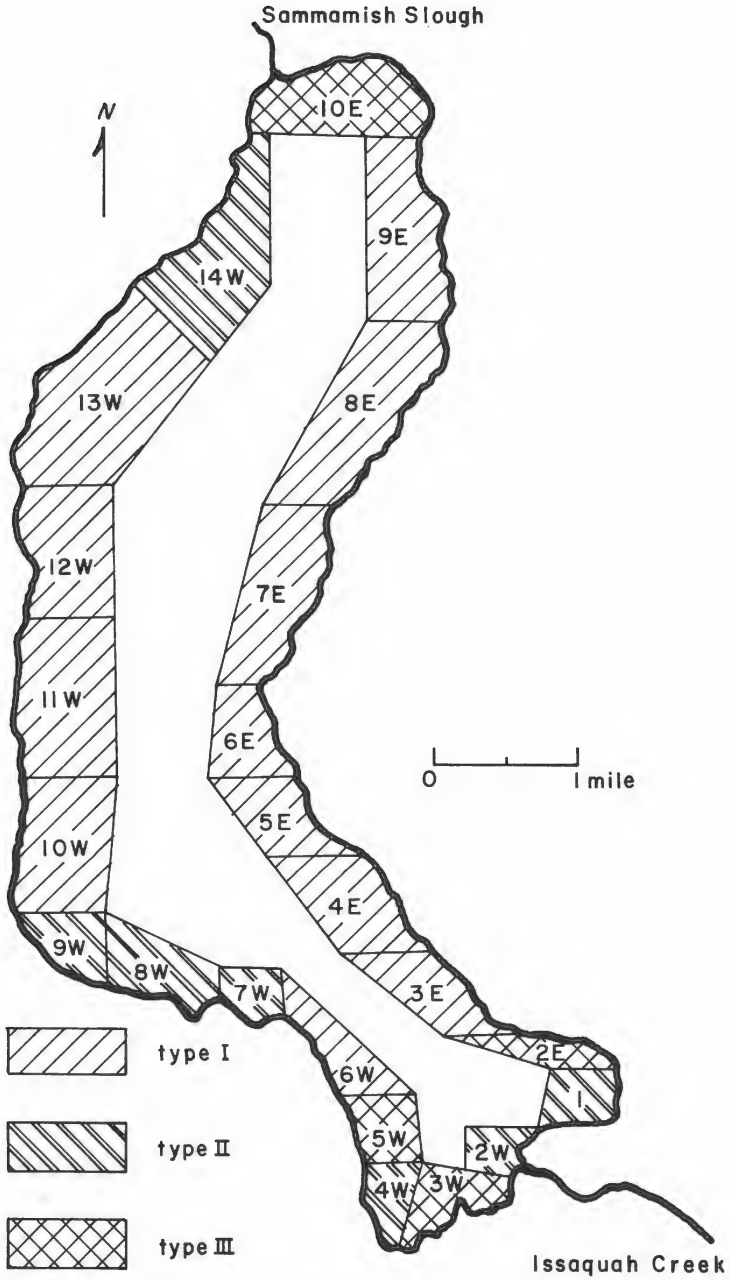

Figure 1. Map of Lake Sammamish (King County, Washington) showing the 23 lake sections used during the study with the location and distribution of the three different shoreline habitat types. (See Table 1 for an explanation of the three habitats.)

body length for that scale measurement. The body-scale relationship in smallmouth bass was linear.

The food and feeding preferences of smallmouth bass were determined through a numerical analysis in which the number of each prey type in each stomach was counted (Windell 1971). These were summed to yield a total for each food type in the entire sample, and a grand total for all items. The totals gave the representative percentage, by number, of each prey type consumed. This method also furnished data that were used to determine the seasonal variation in food types and associated feeding rates. Prey lengths (cm) were used to evaluate food size specificity for smallmouth bass age groups. As an alternative to killing smallmouth bass, a pulsed gastric lavage technique described by Foster (1977) was modefied to remove all stomach contents (Pflug 1981).

Spawning surveys were conducted along the lake shoreline periodically between April and July in 1979 and 1980. Bass nest sites were counted by lake section and water depth, substrate type, and cover type were recorded for each nest. Smallmouth bass nests were distinguished visually by identifying the adult species in attendance.

Results

Age and Growth

The majority of the smallmouth bass population was composed of 2- and 3- year-old fish, representing 39 and 24 percent of the total sample, respectively (Fig. 2). Smaller percentages of the population were composed of 1-year-olds (14 percent), 4-year-olds (12 percent) and 5-year-olds (6 percent), while 6- and 7-year-olds combined represented 5 percent.

Total length ranged from 7 cm to 48 cm. The 2-year-olds, 18 to 23 cm long, clearly represented the major year class in 1979, which predictabily became a major year class in 1980 as 3-year-old fish. A small year class was represented by the 3-year-old fish in 1979 and 4-year-old fish in 1980. The prominent 4-year-olds of 1979 still composed the largest group older than 3 in 1980.

The back-calculation procedures conducted on all year classes to determine lengths at various ages showed that mean total lengths increased rapidly from the 10.1-cm average for 1-year-olds to average 18.5, 26.0, 31.4, 35.7 38.3, and 41.4-cm for each successive year class (Fig. 3). The annual growth curve for Lake Sammamish smallmouth bass in 1979-1980 combined reaveals the exceptionally good growth of these fish compared to smallmouth bass in other waters of North America (Fig. 3). The length-weight relationship mode $W = aL^b$, with $b = 3.0$, demonstrates that young smallmouth bass gain additional weight but length progression is depressed (Fig. 4).

Food and Feeding Habits

Sculpins (*Cottus* sp.) were the major prey item for age one bass, although juvenile salmon and crayfish (*Pasifastacus leniusculus*) were eaten also (Table 1). Surprisingly, no aquatic insects were observed in the stomachs of yearling bass. Smallmouth bass between ages 2 and 3 fed most on sculpins, while 4- and 5-year-olds most frequently ate crayfish and juvenile salmon. Aquatic insects were most abundant in age 2 fish. Incidental prey items included zooplankton, smallmouth bass fry, sqawfish (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), and brook lamprey (*Lampetra richard-*

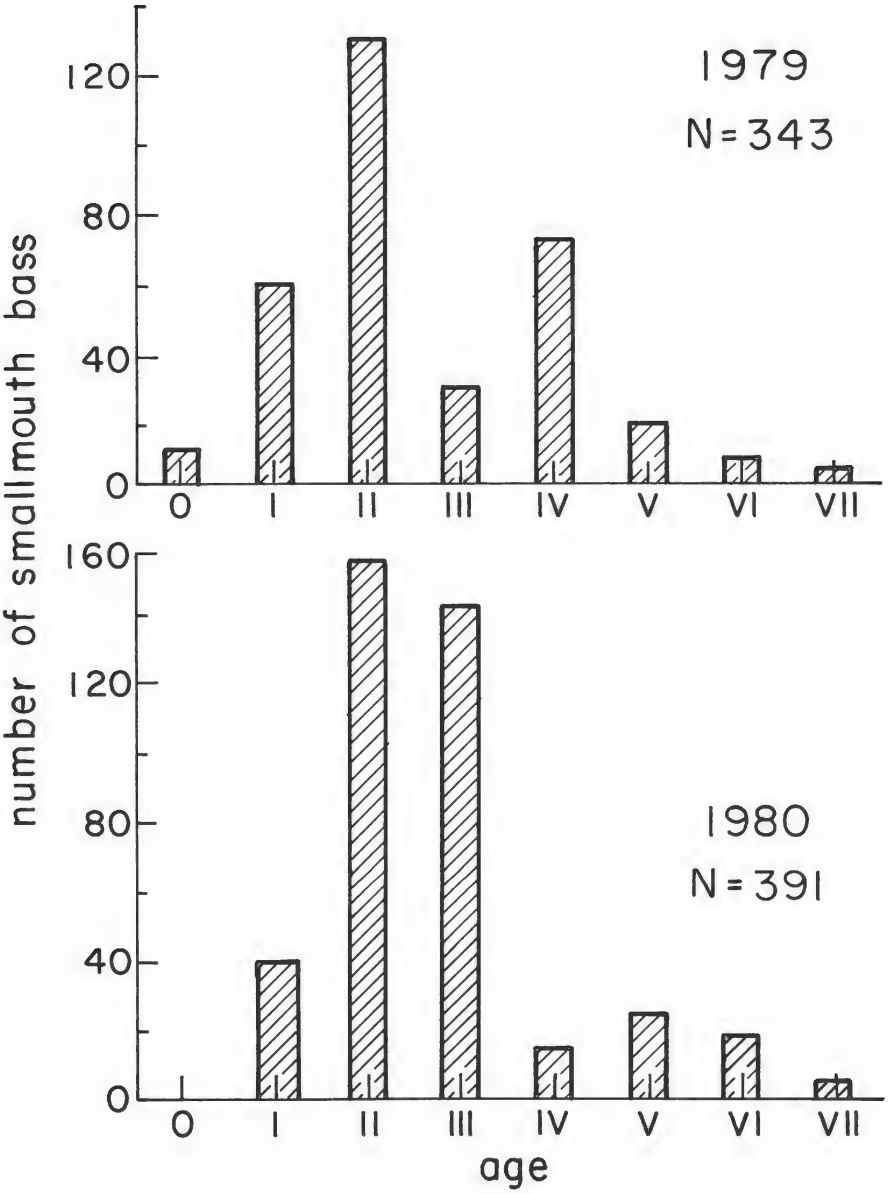

Figure 2. Age group for smallmouth bass captured during the 1979 and 1980 sampling periods.

soni). Partly digested unidentifiable fish made up a large percentage of the prey items in all age groups of smallmouth bass.

Monthly changes in the diet of smallmouth bass for April-July showed a marked

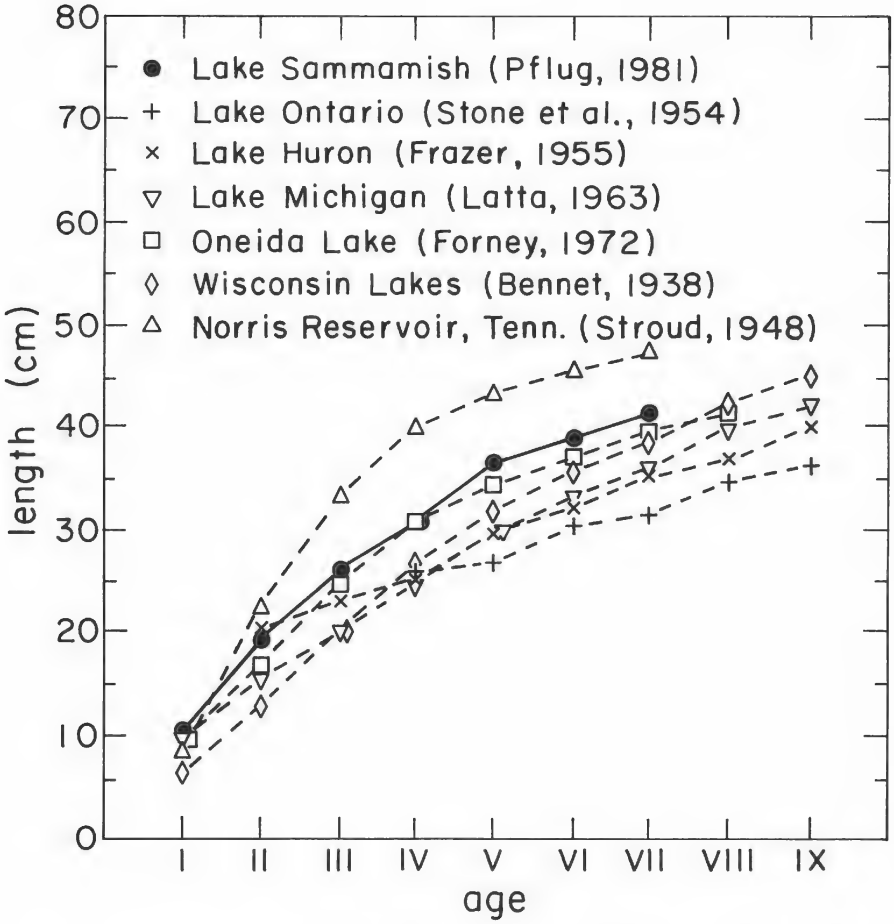

Figure 3. A comparison of growth rates from seven different populations of smallmouth bass in North America.

TABLE 1. Total prey items taken from the stomachs of each smallmounth bass age group during March-August, 1979-80.

	Age				
Prey Item	I	II	III	VI	V
Salmonid	5	42	12	20	10
Sculpin	11	67	50	15	6
Crayfish	2	44	38	24	16
Aquatic insects	0	54	13	2	0
Unidentified fish	5	47	34	16	8
Total No. stomachs examined	30	286	192	72	38
Percent empty stomachs	33%	61%	61%	64%	50%

TABLE 2. Total number of prey items counted in smallmouth bass stomachs for each month, April-July, 1979-80.

Prey items	Month			
	April	May	June	July
Salmonid	7	76	25	8
Sculpin	2	30	24	93
Crayfish	15	36	27	47
Aquatic insects	14	35	38	2
Unidentified fish	7	52	54	26
Total prey items	44	229	168	176
Total number stomachs examined	93	217	205	170
Percent empty stomochs	37%	59%	57%	72%

importance of salmon in May (Table 2). This prominence was a result of the outmigration of young salmon from the Issaquah hatchery at the south end of the lake. Crayfish and sculpins made up the majority of food items observed in July. There was a dramatic increase in feeding that occurred between April and May and continued at a high level through July (Table 2).

Prey size preference was determined by measuring the total length of the recovered prey items to the nearest centimeter. Smallmouth bass selected prey items in relation to their size, with a preference toward progressively larger prey items of all types (Fig. 5). A positive, linear relationship existed between the prey size consumed and the size of the smallmouth bass, which was best described by the linear regression function:

$$Y = 2.596 + 0.793\,X$$

where, Y = size of the prey item

X = age group of the smallmouth bass

The correlation coefficient of 0.374 was significant ($P < 0.05$).

Habitat Preference

Three clearly definable shoreline habitat types exist in Lake Sammamish (Fig. 1 and Table 3). Type I habitat made up approximately 65 percent of the shoreline, which was characterized by a hard substrate, combined with a drop-off from an overbank, and the absence of aquatic vegetation. Approximately 25 percent of the littoral area available in the lake was classed as Type II habitat, characterized by sand or gravel substrate, light to dense growths of aquatic vegetation, with a gradual or moderate depth profile that terminated with steep drop-offs. Type III habitat, which made up approximately 10 percent of the littoral area, possessed moderate to dense aquatic vegetation in shallow water over silt and sand substrate, and was located exclusively at the northern and southern ends of the lake.

Smallmouth bass display a definite predilection for shoreline areas devoid of vegetation and composed of gravel and cobble that had a gradual slope with a drop-off (Table 3). The 12 areas classed as Type I produced 599 of our smallmouth bass; the 7 Type II areas yielded 85 smallmouth bass; and the 4 Type III areas produced only 11 smallmouth bass (Table 3).

Typical smallmouth bass spawning areas also were categorized as Type I habitat (Table 3). The preferred spawning substrate consisted of gravel and cobble devoid of

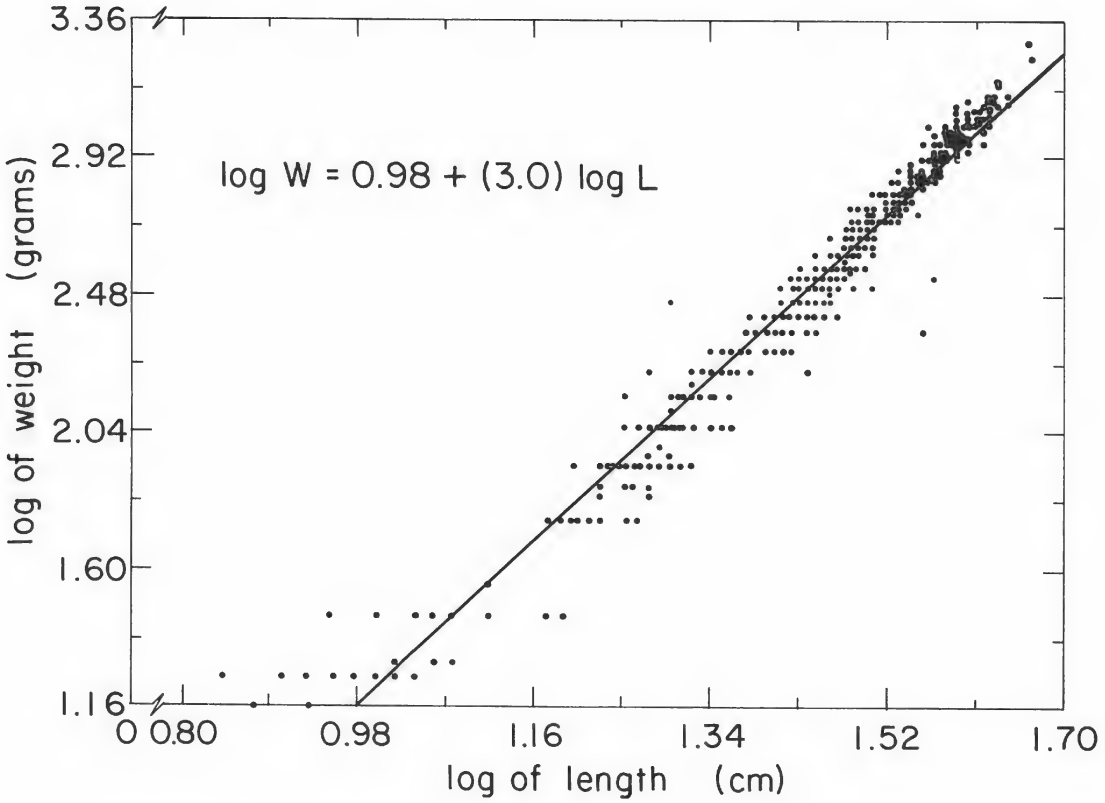

Figure 4. Length-weight relationship for smallmouth bass sampled in 1979-1980.

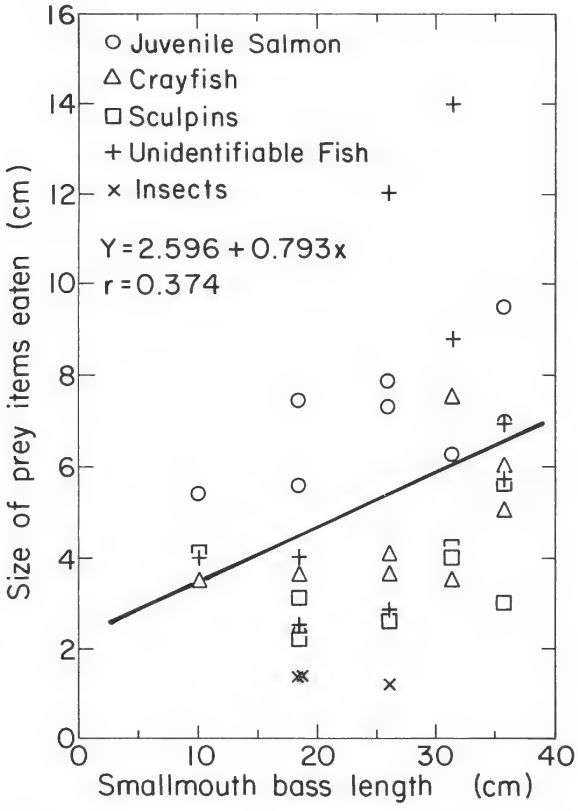

Figure 5. Relationship between the size of various prey items eaten and the size of smallmouth bass. Data points are group means of different food items observed in each age group of smallmouth bass in either 1979 or 1980.

aquatic vegetation. However, nest sites were typically associated with a benthic structure such as an isolated boulder, log, or dockpiling. Nest depths ranged from 1 to 4 meters, but most were in 1.5 to 2.5 meters of water. Counts of nest sites showed that spawning began in early May, peaked late May, and ended in mid-June. May and June surface water temperatures ranged between 13°C and 17°C. The major spawning areas of smallmouth bass were along the eastern shore of the lake from Section 3E northward to Section 9E (Fig. 1), where 125 nest sites were counted during spawning in 1979 and 1980. The western shore from Section 9W northward to Section 14W was a less important spawning area and contained 45 smallmouth bass nests during the two-year study period. Type I habitat accounted for 85 percent of the nests observed (Table 3).

Discussion

Growth rates of smallmouth bass in Lake Sammamish were exceptionally rapid when compared with growth rates reported for this species in other regions of North America (Fig. 3). Faster growth has been observed only by Stroud (1948). The rapid growth

TABLE 3. Habitat and spawning areas of smallmouth bass in Lake Sammamish during 1979 and 1980.

Section	Number of fish sampled	Number of nests counted	Substrate type	Depth profile type[1]	Aquatic vegetation density	Habitat type[2]
1	20	7	sand :gravel	2	moderate	II
2E	2	0	gravel :cobble	2	moderate	III
3E	65	14	gravel :cobble	3	absent	I
4E	80	7	gravel	3	absent	I
5E	47	18	gravel :cobble	3	absent	I
6E	90	13	gravel :cobble	3	absent	I
7E	138	24	gravel :cobble	3	absent	I
8E	60	28	gravel :cobble	3	absent	I
9E	88	21	gravel :cobble	3	absent	I
10E	0	0	silt	1	dense	III
2W	20	0	sand	3	light	II
3W	9	0	silt	3	dense	III
4W	3	4	sand :gravel	1	moderate	II
5W	0	0	silt	3	dense	III
6W	8	3	gravel	3	light	I
7W	7	0	sand :gravel	2	moderate	II
8W	12	4	gravel	3	moderate	II
9W	18	7	gravel :cobble	2	light	II
10W	2	8	gravel :cobble	3	absent	I
11W	1	9	gravel :cobble	3	absent	I
12W	16	5	gravel :cobble	4	absent	I
13W	4	7	gravel :cobble	4	absent	I
14W	5	9	sand :gravel	2	moderate	II

[1]Depth Profile Types: (1) Shallow flats
(2) Gradual slope
(3) Drop-off from overbank
(4) Drop-off from shoreline

[2]Habitat Types: (I) Hard substrate, drop-off, lack aquatic vegetation.
(II) Sand or gravel, gradual depth profile leading to a drop-off, varying aquatic vegetation.
(III) Silt or sand, shallow depth, dense aquatic vegetation.

in Lake Sammamish is probably attributable to an excellent food supply, abundant suitable habitat, favorable water temperatures, and a presumed lack of competitive and predatory fish species (Pflug 1981). The two most important influences on growth are probably temperature and abundant food (Coble 1975). Lake Sammamish appears to have both at optimal levels.

Studies conducted on the Columbia River have shown that within this geographical area smallmouth bass sometimes attain an age of 12 years (Henderson and Foster 1956). The oldest smallmouth bass captured in Lake Sammamish had just begun its eighth growing season. The exact introduction date of smallmouth bass into the lake is unknown, but smallmouth bass did not begin to appear in angler catches until the early 1970s (Pflug 1981). Johnson and Hale (1977) observed that smallmouth bass do not reach maximum abundance until 9-15 years after introduction into new lakes. Therefore, Lake Sammamish may be 2-5 years away from its maximum potential as a producer of smallmouth bass.

Littoral water temperatures in Lake Sammamish ranged from 13°C to 25°C during the smallmouth growing season (Pflug 1981), indicating that growth occurs over a broad range of temperatures, as observed by other investigators (Coble 1967, Wrenn 1980). Although total annual growth and water temperature are probably related, it

appears that factors other than temperature are important in influencing growth in smallmouth bass, especially in older fish (Coble 1967).

In Lake Sammamish, the major prey of smallmouth bass were juvenile salmon, crayfish, and sculpins, with young smallmouth bass feeding primarily on smaller versions of the same prey types that the adults fed on, rather than different food types. Prey size and smallmouth bass size were positively correlated in Lake Sammamish. In other waters, the diet of smallmouth bass changes from small to large items, but often involves a distinct shift of food type as the fish grow larger. Often there is a progression from zooplankton to insects to small fish, finally culminating in crayfish and larger fish (Coble 1975). Guillory (1979) claimed that this shift in type of prey is due to the size of the prey selection rather than any other factors. However, this does not appear to be the case with smallmouth bass in Lake Sammamish, which showed a size preference in the prey selected at all ages with a distinct prey type preference noted only during the month of May, when migratory juvenile salmon were abundant.

Salmon are not abundant in April and July, because release from the Issaquah hatchery has not taken place yet in April, while in July outmigration from Lake Sammamish is completed. As would be expected, the number of salmon in the stomachs of smallmouth bass was lowest in April and July, and highest in May and June.

Resident trout did not appear in any of the smallmouth bass stomachs (Pflug 1981). Bass in other waters do not appear to selectively feed on trout or salmon (Lachner 1950, Stocek and McCrimmon 1965, Warner *et al.* 1968). However, it has been shown that an influx of young salmon or trout into a body of water will yield a higher than normal predation rate by smallmouth bass (Warner 1972), largemouth bass (*Micropterus salmoides*) (Stocek and McCrimmon 1965, Warner 1972), spotted bass (*Micropterus punctulatus*) (Axon 1971), and striped bass (*Morone saxatilis*) (Deppert 1979). Similarly, the influx of a large number of vulnerable salmon smolts into a system like Lake Sammamish should aid in accelerating predation by smallmouth bass and may be a major reason for the excellent growth of Lake Sammamish smallmouth bass.

Smallmouth bass in Lake Sammamish are apparently feeding "generalists" that follow the "numbers maximizer" feeding strategy, which assumes that the predator eats prey items as they are encountered, so that the most numerous prey in the environment should be the most numerous in the stomach (Gfriffiths 1975). This theory assumes that prey size and abundance are the only factors of importance to predators.

Smallmouth bass were observed spawning during the months of May and June in both 1979 and 1980, when water temperatures ranged from 13°C to 18°C in Lake Sammamish (Pflug 1981). Similar spawning temperatures were reported by Stone *et al.* (1954) from Lake Ontario. Although an occasional smallmouth bass was taken from heavily vegetated Type III habitat, smallmouth spawning nests were never observed in that type of habitat. Lake Sammamish bass utilized gravel and cobble shoreline areas devoid of aquatic vegetation for nest building sites, which usually were situated next to some isolated object such as a rock, piling, or log. This is the same situation that Vogele (1980) observed with smallmouth bass in Bull Shoals Reservoir. Smallmouth bass spawning nests generally appear to be made in water less that 2 m deep (Watson 1965, Schneberger 1977), but deeper nests have been noted (Forney 1972, Vogele 1980), which are considere atypical for this species and attributed to heavy wave action occurring during spawning combined with extreme water clarity. Lake Sammamish small-

mouth bass probably spawn at 2 to 4 m depths because of the extremely clear water and severe wave action created by heavy boat traffic on the lake during May and June.

Smallmouth bass in Lake Sammamish exhibited unmistakable habitat preferences for gravel and cobble substrate with access to drop-offs. Habitat of this type appears to be preferred by smallmouth bass in many areas of the United States (Munther 1970, Schneberger 1977, George and Hadley 1979, Hubert and Lackey 1980). This preference for rocky habitat is possibly thought to be due to the preference smallmouth bass have for crayfish in some areas (Munther 1970, Johnson and Hale 1977). We did not detect a distinct preference for crayfish by smallmouth bass in Lake Sammamish. Juvenile salmon frequented the littoral area of the entire lake (Pflug 1981), and sculpins were found on all substrate types without preference for gravel or rock (Richard 1980). Since salmoids, sculpins, and crayfish make up most of the diet of smallmouth bass, it appears that food items are not the major reason for the distinct smallmouth bass preference of gravel and rock in Lake Sammamish. Watson (1965) noted a strong need by smallmouth bass for gravel to spawn, and this may be the determining factor for habitat preference in Lake Sammamish since an abundant food supply exists in the rocky areas also. Smallmouth bass show an extremely strong home area tendency in Lake Sammamish (Pflug and Pauley 1983), and this may be related to the availability of adequate spawning habitat combined with an abundant and accessible food supply.

Literature Cited

Axon, J. R. 1971. An evaluation of the trout fishery in Lake Cumberland, Kentucky, pp. 235-242, *In* G. E. Hall (ed.), Reservoir Fisheries and Limnology, Amer. Fish. Soc. Spec. Publ. No. 8, Washington, D.C.

Bennett, G. W. 1938. Growth of smallmouth black bass, *Micropterus dolomieui*, in Wisconsin waters. Copeia 4: 157-169.

———. 1970. Management of Lakes and Ponds. Van Nostrand Reinold Co., New York, N.Y. N.Y.

Campbell, R. S. and A. Witt. 1953. Impressions of fish scales in plastic. J. Wildl. Manage. 17: 218-219.

Coble, D. W. 1967. Relationship of temperature to total annual growth in adult smallmouth bass. J. Fish. Res. Board Can. 24: 87-99.

———. 1975. Smallmouth bass, pp. 21-23, *In* H. Clepper (ed.), Black Bass Biology and Management. Sport Fishing Institute, Washington, D.C.

Deppert, D. L. 1979. Effect of striped bass predation on an Oklahoma trout fishery. Proc. Ann. Conf. South. Assoc. Fish and Wildl. Agenc. 33: 384-392.

Forney, J. L. 1972. Biology and management of smallmouth bass in Oneida Lake, New York. N.Y. Fish game J. 19: 132-154.

Foster, J. R. 1977. Pulsed gastric lavage: An efficient method of removing the stomach contents of live fish. Prog. Fish Cult. 39: 166-169.

Fraser, J. M. 1955. The smallmouth fishery of South Bay, Lake Huron. J. Fish. Res. Board Can. 12: 147-177.

George, E. G., and W. F. Hadley. 1979. Food and habitat partitioning between rock bass (*Amblo-plites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Trans. Amer. Fish. Soc. 108: 243-261.

Goodpasture, J. M. 1979. Aquatic plants in selected waters of King County. METRO (Municipality of Seattle), Water Quality Division Report, Seattle, Wash.

Griffiths, D. 1975. Prey availability and the food of predators. J. Animal Ecol. 56: 1209-1214.

Guillory, V. 1979. Analysis of prey selection in chain pickerel. Proc. Ann. Conf. South. Assoc. Fish and Wildl. Agenc. 33: 507-517.

Henderson, C., and R. F. Foster. 1956. Studies of smallmouth black bass (*Micropterus dolomieui*) in the Columbia River near Richland, Washington. Trans. Amer. Fish. Soc. 86: 112-127.

Hubert, W. A., and R. T. Lackey. 1980. Habitat of adult smallmouth bass in a Tennessee River reservoir. Trans. Amer. Fish. Soc. 109: 364-370.

Johnson, F H., and J. G. Hale. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieui*) in four northeastern Minnesota lakes 1948-1969. J. Fish. Res. Board Can. 34: 1626-1632.

June, J. A. 1979. Scale (Backcal). Fisheries Research Institute, Univ. Washington, Seattle. Program No. FRI 365.

Keating, J. F. 1970. Growth Rates and Food Habits of Smallmouth Bass in the Snake, Clearwater and Salmon Rivers, Idaho, 1965-1967. Univ. Idaho, Moscow. M.S. Thesis.
Lachner, E. A. 1950. Food, growth and habits of fingerling northern smallmouth bass, *Micropterus dolomieui* Lacepede, in trout waters of western New York. J. Wildl. Manage. 14: 50-56.
Latta, W. C. 1963. The life history of the smallmouth bass (*Micropterus dolomieui*) at Wangoshance Point, Lake Michigan. Mich. Dept. Conserv. Bull. Instit. Fish Res. No. 5.
Montgomery, J. C., D. H. Fickeisen, and C. D. Becker. 1980. Factors influencing smallmouth bass production in the Hanford Area, Columbia River. Northw. Sci. 54: 296-305.
Munther, G. L. 1970. Movement and distribution of smallmouth bass in the middle Snake River. Trans. Amer. Fish. Soc. 99: 44-53.
Pflug, D. E. 1981. Smallmouth Bass (*Micropterus dolomieui*) of Lake Sammamish: a Study of Their Age and Growth, Food and Feeding Habits, Population Size, Movement and Homing Tendencies, and Comparative Interactions with Largemouth Bass. Univ. Washington, Seattle. M.S. Thesis.
———, and G. B. Pauley. 1983. The movement and homing of smallmouth bass, *Micropterus dolomieui*, in Lake Sammamish, Washington. Calif. Fish Game, 69: 207-216.
Richard, N. A. 1980. Life Hostory and Population Characteristics of the Prickly Sculpin (*Cottus asper* Richardson) in Lake Washington. Univ. Wash. Seattle. M.S. Thesis.
Schneberger, E. 1977. Smallmouth bass life history, ecology and management. Wis. Dept. Nat. Res. Publ. No. 16-3600(77).
Stocek, R. F., and H. R. McCrimmon. 1965. The co-existence of rainbow trout (*Salmo gairdneri* Richardson) and largemouth bass (*Micropterus salmoides* Lacepede) in a small Ontario lake. Can. Fish. Cult. 35: 37-58.
Stone, U. B., D. G. Pasko, and R. M. Roecker. 1954. A study of Lake Ontario-St. Lawrence River smallmouth bass. N.Y. Fish Game J. 1: 1-26.
Stroud, R. H. 1948. Growth of the basses and black crappie in Norris Reservoir, Tennessee. J. Tenn. Acad. Sci. 23: 31-99.
Vogele, L. E. 1980. Reproduction of smallmouth bass, *Micropterus dolomieui*, in Bull Shoals Lake, Arkansas. U.S. Fish Wildl. Serv. Tech. Paper 106.
Warner, K. 1972. Further studies of fish predation of salmon stocked in Maine lakes. Prog. Fish Cult. 34: 217-221.
———, R. P. AuClair, S. E. DeRouche, K. A. Harvey, and C. F. Ritzi. 1968. Fish predation on newly stocked landlocked salmon J. Wildl. Manage. 32: 712-717.
Watson, J. E. 1965. The Maine Smallmouth. Maine Dept. Inland Fish and Game, Fish Res. Bull. No. 3.
Windell, J. T. 1971. Food analysis and rate of digestion, pp. 215-226 *in* W. E. Richard (ed.), Methods for Assessment of Fish Production in Fresh Waters. Internatl. Biol. Progr. Handbook 3. Blackwell Scientific Publications, Oxford, U.K.
Wrenn, W. B. 1980. Effects of elevated temperature on growth and survival of smallmouth bass. Trans. Amer. Fish. Soc. 109: 617-625.

Received June 21, 1982
Accepted for publication February 15, 1983

Albert J. Parker

Geography Department
University of Georgia
Athens, Georgia 30602

A Comparison of Structural Properties and Compositional Trends in Conifer Forests of Yosemite and Glacier National Parks, USA

Abstract

Structural properties (density, stand basal area, and mean diameter) are compared between forests of Yosemite National Park, California, and Glacier National Park, Montana, as well as among forest types within regions. Forest types within Glacier display markedly disparate structures, whereas those within Yosemite possess similar structures. Furthermore, two of the three Glacier forest types are characterized by pronounced compositional differences between small and large size classes. In Yosemite, each forest type has a similar composition in both the small and large size classes. These geographic differences in forest structure and compositional trend are attributed to distinctive fire patterns in each region. In Yosemite, the strength and consistency of summer drought stress favor a surface fire regime in all forest types sampled, promoting uniformity of structure and compositional dynamics among Yosemite forests. In Glacier, site microclimates mitigate or exacerbate occasional dry summers, resulting in a broader spectrum of disturbance regimes among forest types, ranging from frequent surface fires on dry, open flats, through crown fires on intermediate settings, to infrequent fires on mesic, sheltered slopes. The diversity of disturbance regimes promotes heterogeneity of structure and complex patterns of compositional dynamics among Glacier forests.

Introduction

Forest structure can be characterized in several ways, each with a different type of data. One approach is to examine the morphology of the species of which the community is composed (Knight and Loucks 1969). A second involves analyzing gross structural features of the entire community, such as density, stand basal area, and mean diameter, and comparing these features among sampling units (Goff and Zedler 1968). A third approach uses size/age class data to infer population trends (Whipple and Dix 1979). The writer has used the species-morphology approach previously to examine the structural dissimilarities of conifer forest of Yosemite National Park, California, in the central Sierra Nevada, and of Glacier National Park, Montana, in the northern Rocky Mountains (Parker 1982). He found that the variability of morphological features within Yosemite forests corresponds to an environmental gradient dominated by elevation. In Glacier, on the other hand, temporal differences among stands related to distinctive fire regimes obscure the direct expression of environmental influence on forest morphology. In this paper, forest structures in the two areas are compared in terms of density, basal area, and mean diameter among stands, as well as by compositional trends across size classes.

Three forest types are recognized in each region based on patterns of canopy dominance among individual stands (Table 1; cf. Parker 1982). In Yosemite, *Pinus ponderosa/Calocedrus decurrens* (ponderosa pine/incense-cedar) forests occur on xeric, lower elevation (1200-1900 m) sites; *Abies concolor/Calocedrus decurrens* (white fir/incense-cedar) forests occupy mesic, lower elevation sites; and *Abies magnifica/Abies concolor* (red fir/white fir) forests, with locally important *Pinus jeffreyi* (Jeffrey pine)

TABLE 1. Tree species composition by forest type.

YOSEMITE
Pinus ponderosa/Calocedrus decurrens:
Pinus ponderosa Laws.
Calocedrus decurrens (Torr.) Florin
Pinus lambertiana Dougl.
Quercus kelloggii Newb.
Abies concolor (Gord. and Glend.) Lindl.
Abies concolor/Calocedrus decurrens:
Abies concolor
Calocedrus decurrens
Pinus lambertiana
Pinus ponderosa
Quercus kelloggii
Abies magnifica A. Murr.
Cornus nuttallii Aud.
Abies magnifica/Abies concolor:
Abies magnifica
Abies concolor
Pinus contorta ssp. **murrayana** (Engelm. ex Wats.) Critchfield
Pinus jeffreyi Grev. and Balf.
Pinus monticola Dougl.
Pinus lambertiana
GLACIER
Pinus ponderosa/Pseudotsuga menziesii
Pinus ponderosa
Pseudotsuga menziesii (Mirb.) Franco
Pinus contorta ssp. **latifolia** (Balf.) Critchfield
Larix occidentalis Nutt.
Picea engelmannii/glauca complex (see Habeck and Weaver 1969, Daubenmire 1974)
Pinus contorta/Larix occidentalis:
Pinus contorta ssp. **latifolia**
Larix occidentalis
Pseudotsuga menziesii
Picea engelmannii/glauca
Betula papyrifera Marsh.
Populus tremuloides Michx.
Thuja plicata/Tsuga heterophylla:
Thuja plicata Donn
Tsuga heterophylla (Raf.) Sarg.
Larix occidentalis
Pinus monticola
Picea engelmannii/glauca
Populus trichocarpa Torr. and Gray
Betula papyrifera

Species are listed in order of importance by forest type.

and *Pinus contorta* ssp. *murrayana* (lodgepole pine) populations, are found at higher elevations (1900-2400 m) (cf. Rundel *et al.* 1977). In Glacier, upland forest types are arranged along a locally-controlled moisture/fire frequency gradient, with *Pinus ponderosa/Pseudotsuga menziesii* (ponderosa pine/Douglas-fir) forests on somewhat xeric sites, *Pinus contorta* ssp. *latifolia/Larix occidentalis* (lodgepole pine/western larch) forests on intermediate settings, and *Thuja plicata/Tsuga heterophylla* (western redcedar/western hemlock) forests on mesic sites (cf. Pfister *et al.* 1977, Kessell 1976). (See Table 1 for taxonomic authorities.)

Strong seasonality of precipitation on the western flank of the Sierra Nevada contrasts with the weak seasonality of precipitation west of the Continental Divide in Glacier (Fig. 1). Greater than one-half of the annual precipitation in Yosemite falls

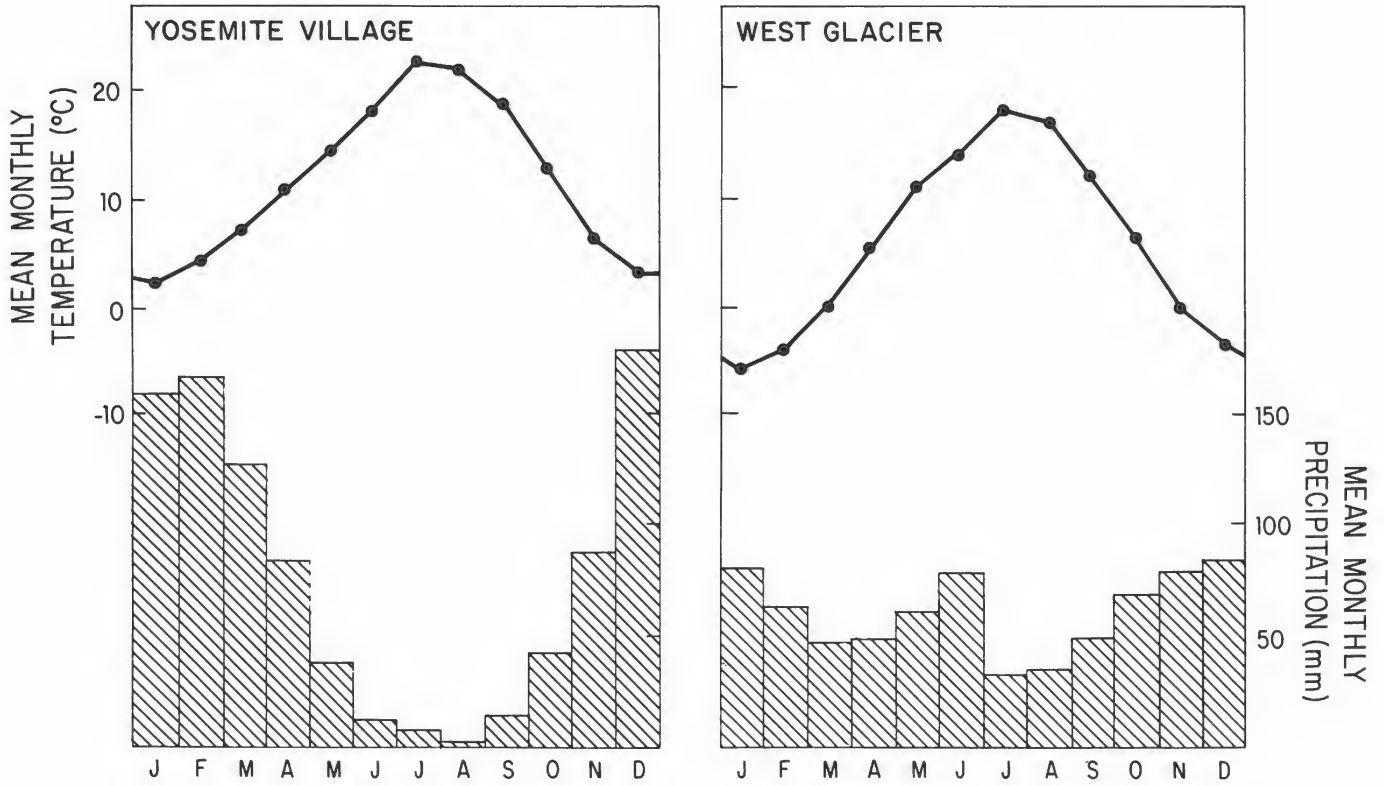

Figure 1. Thirty year means of monthly temperature and precipitation for Yosemite Village, California, and West Glacier, Montana. Source: National Oceanic and Atmospheric Administration, 1978.

from January through March, when upper level westerly flow induces frequent passage of cyclonic storms. Summers are characterized by chronic drought, because of the persistent anchoring of the North Pacific subtropical high pressure cell off the coast of California. Conversely, the year-round penetration of cyclonic systems inland from the North Pacific provides Glacier with a more uniform precipitation regime. The July/August precipitation minimum reflects occasional dry years when the subtropical anticyclone is either atypically strong or displaced poleward.

Chronic summer drought in Yosemite favors a surface fire regime throughout montane and lower subalpine forests; the recurrence interval of these surface fires in presettlement times apparently lengthened with increasing elevation. In spite of interruption by fire suppression, the prevalence of surface fires appears to have promoted structural similarity among Yosemite forests types. In Glacier, occasional summer drought can be reinforced or mitigated by site microclimates, allowing a greater variety of characteristic disturbance regimes among forest types. On drier, open sites (whether induced by aspect, sandy substrates, or grazing history) surface fires are common. On somewhat more mesic slopes and flats, stand-destroying crown fires are more common. On sheltered mesic slopes (often exhibiting a local-scale lake-influence) fires are uncommon events. This diversity of fire regimes manifests itself in structural dissimilarities among Glacier forest types.

Methods

In Yosemite, 30 stands were sampled within the 1220 to 2440 m elevation range, whereas in Glacier 18 stands between 910 and 1370 m elevation were sampled. In both regions, attempts were made to collect samples from a variety of slope aspects and gradients. Criteria employed to select stands included gross environmental and compositional homogeneity as assessed by field inspection, uniformity of the canopy, dominance by conifers, and exclusion of riparian sites. Samples in each stand consisted of twenty circular quadrats (5.64 m radius) located within a 60 x 75 m grid system by a stratified systematic unaligned sampling technique (Berry and Baker 1968). Within each 1/100 ha quadrat, the species and basal area at breast height (1.4 m) were recorded for all trees with stems 10.2 cm or greater in basal diameter. These data were summarized to yield structural properties, including tree density, total basal area, and mean tree diameter for each stand.

Results

Density-Basal Area-Diameter Relationships. The forests of Yosemite (Y) are less dense than those of Glacier (G), yet they generally support a greater standing biomass and are composed of individuals of larger girth (Table 2). In both regions, as expected, mean diameter and tree density exhibit a strong negative correlation ($r_Y = -0.848$, $p < 0.01$; $r_G = -0.741$, $p < 0.01$). This is because within closed forests, as individual trees grow, they progressively utilize or assimilate a greater proportion of the available nutrient, light, and water resources. Hence, biomass becomes concentrated in a few, large individuals (cf. Waring and Franklin 1979). In addition, the correlation between mean diameter and stand basal area is positive among both Yosemite and Glacier stands, although the correlation coefficient for Glacier is weak ($r_Y = 0.639$, $p < 0.01$; $r_G = 0.331$, $p < 0.2$).

The relationship among density, basal area, and diameter within each forest type clarifies comparisons between regions based on collective data; averaged values of these properties are presented for the six forest types (Table 2). A comparison of averaged values for each forest type in Yosemite (using the Mann-Whitney U-test) indicated

TABLE 2. Structural properties of Yosemite and Glacier forests.

	Tree Density (stems. ha^{-1})	Basal Area (dm^2. ha^{-1})	Mean Diameter (cm)
YOSEMITE:			
All stands	544 ± 90*	7802 ± 773	45.9 ± 4.7
Forest types:			
Pinus ponderosa/Calocedrus (n = 8)	714 ± 290	6564 ± 913	38.5 ± 12.0
Abies concolor/Calocedrus (n = 9)	563 ± 191	7883 ± 1381	44.5 ± 7.9
Abies magnifica/Abies concolor (n = 13)	425 ± 79	8508 ± 1442	51.5 ± 6.0
GLACIER:			
All stands	667 ± 124	4857 ± 825	32.0 ± 4.2
Forest types:			
Pinus contorta/Larix (n = 8)	766 ± 171	3766 ± 673	25.3 ± 1.8**
Thuja/Tsuga (n = 6)	764 ± 137	6665 ± 1326**	33.6 ± 4.9
Pinus ponderosa/Pseudotsuga (n = 4)	323 ± 180**	4327 ± 1357	43.9 ± 12.2

*95% confidence limits based on Student's t distribution are shown.

**Among Glacier forest types, the mean for this type is significantly different ($p < 0.05$, Mann-Whitney U-test) from the other two forest types. There are no significant differences among means of structural properties in Yosemite forests.

that no significant differences in tree density, basal area, or mean diameter existed among types. Hence, gross structural features of Yosemite forests in the montane zone are similar, even among diverse forest types. In Glacier forests, statistically significant differences in average values among forest types were apparent (Table 2). First, the density of the *Pinus ponderosa/Pseudotsuga* type on somewhat xeric sites was significantly lower than forest types on more mesic sites. The open grown character of these stands appears to have been maintained by a presettlement surface fire regime (Lunan and Habeck 1973). Second, basal area was significantly greater in mesic *Thuja/Tsuga* forests than in the other forest types. On the sheltered, northwest facing slopes of the Lake McDonald drainage, local climate and topographic features mitigate the drought conditions associated with periods of low precipitation; fires are thus infrequent, and allow a large accumulation of biomass (Kessell 1976, Anderson 1968). Third, mean diameter was significantly lower in *Pinus contorta/Larix* forests than in the other two forest types. These forests, on dry/mesic sites, appear to represent typical conditions at lower elevations throughout much of the northwestern sector of Glacier. On these sites, stand-destroying crown fires occur episodically, resulting in smaller tree size when compared to the other two Glacier forest types.

Correlations among tree density, basal area, and mean diameter within forest types underscore the patterns described above (Table 3). Small sample sizes for each forest type diminish the likelihood of statistically significant correlations between structural properties within forest types. In view of this observation, only the general pattern of

TABLE 3. Correlation values among structural properties and values of the index of compositional change by forest type.

	Correlation values			Index of Compositional Change
	DENS/DIAM	BA/DIAM	DENS/BA	
YOSEMITE				
All stands	-0.848**	0.639**	-0.271	
Forest types				
Pinus ponderosa/Calocedrus (n = 8)	-0.889**	0.477	-0.136	0.746
Abies concolor/Calocedrus (n = 9)	-0.870**	0.745*	-0.437	0.634
Abies magnifica/Abies concolor (n = 13)	-0.686**	0.624*	-0.123	0.756
GLACIER				
All stands	-0.741**	0.331	0.246	
Forest types:				
Thuja/Tsuga (n = 6)	-0.805	0.729	-0.189	0.764
Pinus contorta/Larix (n = 8)	-0.649	0.181	0.618	0.550
Pinus ponderosa/Pseudotsuga (n = 4)	-0.753	0.032	0.630	0.300

* $p < 0.05$.

** $p < 0.01$

structural correlations in each forest type is emphasized here. In Yosemite forests, where no significant differences were found in inter-type structural comparisons of averaged stands properties, no strong differences in patterns of correlation among these stand properties are apparent. In Glacier forests, however, correlation of structural properties within forest types displays distinctive patterns. *Thuja/Tsuga* forests show a correlation pattern similar to that of Yosemite forests (i.e., a strong positive correlation beween basal area and mean diameter coupled with a weak negative correlation between density and basal area). All of the Yosemite forest types and Glacier's *Thuja/Tsuga* forest type seem to display the influence of competitive thinning on forest structure, with standing crop being maximized in forests with relatively few, but large trees. Glacier's *Pinus ponderosa/Pseudotsuga* and *Pinus contorta/Larix* forest types exhibit correlation patterns unlike Yosemite forests. Both show a rather strong positive correlation between density and basal area, indicating that in these forest types, high density (presumably related to initial stocking levels) accompanies large stand basal area values (cf. Goff and Zedler 1968).

Compositional change within forest types. In order to assess the compositional change within forest types, I developed an index, patterned after the Dynamic Adaptation Values of Peet and Loucks (1977), but altered to provide a single value for each forest type (See Table 3). To determine compositional change index values, trees in each stand were stratified into 10 cm diameter class intervals by species. For all species in each stand with a relative density exceeding five percent, the species' relative density in the smallest tree diameter class (RD_S: 10-20 cm) and species relative density for all larger diameter classes (RD_L: > 20 cm) were computed. Stand index values are based on the ratio of RD_S to RD_L. RD_S/RD_L values of about 1.0 identify species that are comparably represented in both small and large diameter classes; values range toward zero for declining species and toward positive infinity for invading species. Thus,

variation of RD_S/RD_L values from 1.0 in either direction reflects species compositional shifts across diameter classes in the stand. Next, values of RD_S/RD_L exceeding 1.0, representing species apparently increasing in importance, were converted to reciprocals. Consequently, the ratio value will approach zero for any species showing marked differences in representation between small and large size classes, irrespective of the species trend. Index values for entire stands were then calculated by multiplying the RD_S/RD_L value (or its reciprocal) for each species by that species' relative density (thus weighing each species contribution to the index by its commonness in the stand), and summing the resultant values for all species. The final index values for a stand, therefore, range from 1.0 in stands of constant composition across size classes to a hypothetical extreme of 0.0 in stands where there are no shared species in small and large size classes. Compositional change index values reported for each forest type are arithmetic means of index values from each stand in the forest type.

Compositional change index values for Yosemite and Glacier forest types (Table 3) suggest that all Yosemite forest types plus Glacier's *Thuja/Tsuga* forest type (with index values exceeding 0.600 for each type) exhibit less compositional alteration than either the *Pinus ponderosa/Pseudotsuga* or *Pinus contorta/Larix* forest types in Glacier.

Discussion

Although Yosemite forests show compositional and morphological changes with elevation and topographic conditions (Parker 1982), average values of tree density, basal area, and mean diameter for each forest type are similar. Additionally, correlation patterns among these same structural properties are comparable among forest types, suggesting that structural development is similar for all forests sampled. The structural similarity among Yosemite forest types may be, in part, a consequence of the severity of summer drought in the montane zone in Yosemite, which induces pronounced soil moisture deficit (Arkley 1981) and thereby intensifies competitive stress among trees.

The role of fire history in forest structure in the Sierras must also be considered. Many workers have found that the structure of Sierran conifer forests (particulaly the "mixed" conifer forests, which are homologous to *Abies concolor/Calocedrus* forests here) has been changed from presettlement conditions (Bonnicksen and Stone 1981) by a decline in fire frequency associated with a decline in burning by native Indians (ca. 1875) and an aggressive fire suppression policy imposed by land management agencies (ca. 1900) (Kilgore and Taylor 1979). The index of compositional change value for *Abies concolor/Calocedrus* forests (0.634) is lower than for the other two forest types, reflecting the influence of fire frequency alteration on the composition of these mesic lower elevation forests. The virtual exclusion of surface fires has promoted an increase in stem density and an associated compositional shift toward increased dominance by the tolerant *Abies concolor* (Fig. 2) (Vankat and Major 1978). Nevertheless, the fire frequency reduction has existed for about 110 years, and many trees that invaded these stands in the late nineteenth century are dominants or co-dominants of the forest canopy today. Thus, the contrast beween small and larger diameter classes reflected in the compositional change index, which was likely more pronounced several decades ago, has been reduced. The influence of fire frequency alteration on the composition of the other two Yosemite forest types has not been as pronounced, judging from their higher compositional change index values. In xeric, lower elevation

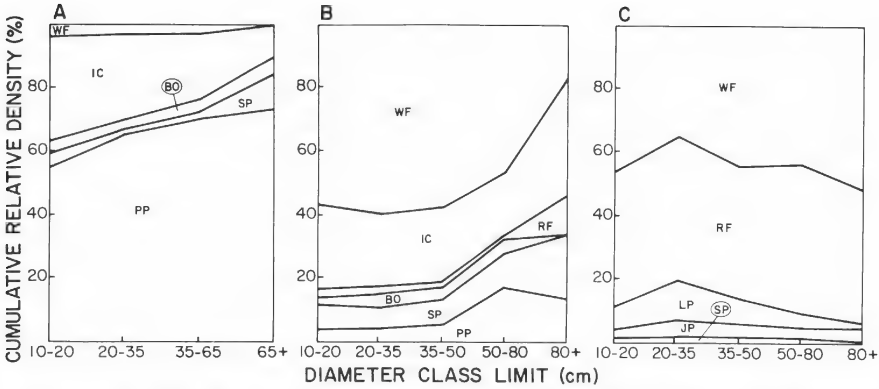

Figure 2. Composite size-class diagrams for forest types in Yosemite. (A) *Pinus ponderosa/Calocedrus,* (B) *Abies concolor/Calocedrus,* and (C) *Abies magnifica/Abies concolor.* species are arranged from most (first) to least (last) shade tolerant: WF—*Abies concolor*; IC—*Calocedrus decurrens*; RF—*Abies magnifica*; BO—*Quercus kelloggii*; LP—*Pinus contorta* ssp. *murrayana*; JP—*Pinus jeffreyi*; SP—*Pinus lambertiana*; PP—*Pinus ponderosa.*

forests, although the importance of the tolerant *Calocedrus decurrens* has increased with fire suppression (Fig. 2), drought stress appears to have allowed the intolerant *Pinus ponderosa* to remain an important element in all diameter classes. In the *Abies magnifica/Abies concolor* forest type at higher elevations, presettlement fires were apparently less common events (Kilgore 1971). Hence, the advent of fire suppression has not greatly influenced patterns of species importance among the codominants of this forest type (Fig. 2).

Glacier forest types exhibit greater dissimilarities in both structural properties and compositional trends than Yosemite forest types. Structural complexity is evident in the significant differences in averaged values of density, basal area, and mean diameter among forest types, as well as in differences in correlation pattern within types.

In the sheltered *Thuja/Tsuga* forests of Glacier, fires are apparently uncommon events. These stands have been free from fire for long periods (at least 150 years: Kessell 1976); disturbance of the forest canopy during this time has been limited to sporadic individual treefalls. The relatively undisturbed canopy configuration promotes progressive thinning of the trees. Both *Thuja plicata* and *Tsuga heterophylla* maintain self-replicating populations on these sites (Fig. 3). Hence, like the Yosemite forests studied, the *Thuja/Tsuga* forest type in Glacier displays both a high value of the compositional change index and a structural correlation pattern indicative of maximum standing crop in mature forests with relatively few, but large individuals.

Fires are more frequent in dry/mesic *Pinus contorta/Larix* forests than in *Thuja/Tsuga* forests (crown fire return interval is perhaps 50-100 years, Kessell 1976, cf. Arno 1980). Moreover, burns often occur as stand-killing crown fires. The frequency and intensity of crown fires in Glacier appears to have been increased by widespread mortality of *Pinus contorta* caused by periodic mountain pine beetle epidemics (Amman and Baker 1972). Following crown fires, open sites are soon recolonized by *Pinus contorta* and *Larix occidentalis,* producing an even-aged forest structure. With time, more tolerant species, such as *Pseudotsuga menziesii* and *Picea engelmannii/glauca*

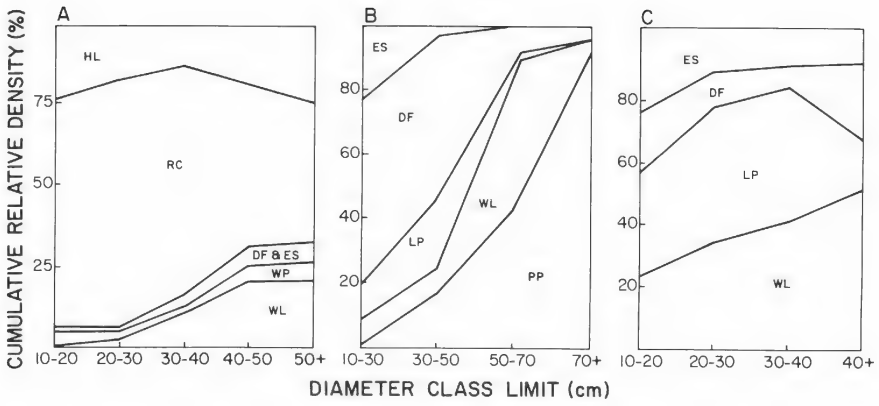

Figure 3. Composite size-class diagrams for forest types in Glacier: (A) *Thuja/Tsuga*, (B) *Pinus ponderosa/Pseudotsuga*, (C) *Pinus contorta/Larix*. Species are arranged from most (first) to least (last) shade tolerant: HL—*Tsuga heterophylla*; RC—*Thuja plicata*; ES—*Picea engelmannii/glauca*; DF—*Pseudotsuga menziesii*; WP—*Pinus monticola*; LP—*Pinus contorta* ssp. *latifolia*; WL—*Larix occidentalis*; PP—*Pinus ponderosa*.

invade the understory, thereby promoting compositional differences between canopy and understory (Fig. 3). In the absence of fire, eventual conversion to *Pseudotsuga menziesii* and *Picea*-complex dominance could be anticipated. Dominance by *Pinus contorta* and *Larix occidentalis* over large areas in Glacier, however, suggests that the fire recurrence interval is typically shorter than the life span of either of these colonizer species (i.e., a century or less). Hence, recurrent crown fires in this region appear to truncate ecosystem recovery during the gradual transition from intolerant to tolerant species dominance. The patchy distribution of crown fires produces a patterned mosaic of different-aged forest stands (Wright 1974) that are characterized, in general, by low compositional stability (the compositional change index value is 0.550). The correlation pattern within the *Pinus contorta/Larix* forests type differs from those of Yosemite or Glacier's *Thuja/Tsuga* forest type. The positive correlation between density and basal area suggests that in this ecosystem, initial density of established trees may play a greater role in dictating biomass accumulation than processes of competitive thinning. Goff and Zedler (1968) found a similar correlation pattern in boreal transition forests of the upper Midwest, which are periodically disturbed by canopy fires and spruce budworm outbreaks (Hett and Loucks 1976). The compositional changes within and structural traits of *Pinus contorta/Larix* forests are characteristic of periodic crown fire regimes.

Pinus ponderosa/Pseudotsuga forests in Glacier were characterized by a presettlement surface fire regime similar in frequency to that of lower elevation Yosemite forests. However, because fire suppression in Glacier has been implemented more recently than in Yosmite (ca. 1910) and was not generally effective in the region until the 1930s (Arno 1980), these previously open-grown *Pinus ponderosa* woodlands still exhibit pronounced compositional alteration, as evidenced by the low index value for this forest type (0.300). Both *Pseudotsuga menziesii* and *Picea*-complex have become established under the *Pinus ponderosa* overstory (Fig. 3), apparently in response to fire suppression (Lunan and Habeck 1973, Habeck and Mutch 1973). *Pinus ponderosa/*

Pseudotsuga forests exhibit a structural correlation pattern similar to that of *Pinus contorta/Larix* forests of Glacier, in that density correlates positively with stand basal area.

In both *Pinus contorta/Larix* and *Pinus ponderosa/Pseudotsuga* forest types, compositional trends within the forest and associated structural properties reflect responses to ecosystem disruption. On the one hand, periodic crown fires in *Pinus contorta/Larix* forests interrupt successional recovery and promote a structure that is greatly influenced by the density of established trees in the post-burn forest. On the other hand, recent suppression of a surface fire regime in *Pinus ponderosa* woodlands has triggered a release of *Pseudotsuga menziesii* and *Picea*-complex populations, producing a pulse of invasive trees which accounts for both the compositional shifts and the increased importance of tree density on standing crop in this forest type. A similar response might be anticipated following exclusion of livestock grazing (Vale 1981), although Lunan and Habeck (1973), studying *P. ponderosa* woodlands in Glacier, never mention grazing as a contributing factor in the development or maintenance of these plant communities.

The differences in compositional trends within and structural characteristics between forest types in Glacier and Yosemite, then, reflect differences in climate, natural fire regimes, and the influence of fire suppression. The variety of structures among forest types in Glacier appears to be related to the differences in natural fire regimes allowed by the modification of regional climate by site factors. For example, on topoedaphically dry sites (south-facing aspects; thin sandy substrates), recent suppression of surface fires has triggered invasion of more tolerant species (*Pseudotsuga menziesii* and *Picea*-complex). On dry-mesic sites covering most slopes in the montane zone of Glacier, sporadic crown fires periodically reinitiate vegetation recovery mechanisms, resulting in a forest type possessing intolerant species (*Pinus contorta* ssp. *latifolia* and *Larix occidentalis*) in the overstory, with varying representations of invasive tolerant species. Mesic, sheltered slopes rarely burn, so that *Thuja/Tsuga* forests in Glacier maintain a forest structure strongly influenced by gradual thinning, a structure more similar to Yosemite forests than to the other Glacier forest types. In Yosemite, more intense summer droughts, by exacerbating moisture stress, induce thinning on most sites. Hence, forest structures are similar throughout the montane zone of Yosemite, although subtle differences in compositional patterns among forest types suggest that the influence of suppression of surface fires has not been uniform.

Acknowledgments

I acknowledge Drs. Thomas R. Vale, Kathleen C. Parker, and Vernon Meentemeyer for advice and critical review of the manuscript. Furthermore, I thank Kathleen C. Parker for assistance in data collection. Funds in support of data collection, analysis, and publication have been provided by a National Science Foundation fellowship, a University of Wisconsin travel grant and fellowship, and the University of Georgia graduate school.

Literature Cited

Amman, G. D., and B. H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. J. For. 70:204-209.

Anderson, H. E. 1968. Sundance fire: an analysis of fire phenomena. U.S. For. Serv. Res. Pap. INT-56.

Arkley, R. J. 1981. Soil moisture use by mixed conifer forest in a summer-dry climate. Soil Sci. Soc. Am. J. 45:423-427.
Arno, S. F. 1980. Forest fire history in the Northern Rockies. J. For. 74:460-465.
Berry, B. J. L., and A. M. Baker. 1968. Geographic sampling, pp. 91-100 *in* Spatial Analysis: a Reader in Statistical Geography. B. J. L. Berry and D. F. Marble (eds.). Prentice-Hall, Englewood Cliffs, N. J.
Bonnicksen, T M., and E. C. Stone. 1981. The giant sequoia-mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. For. Ecol. and Mgt. 3:307-328.
Daubenmire, R. F. 1974. Taxonomic and ecological relationships between *Picea glauca* and *Picea engelmannii*. Can. J. Bot. 52:1545-1560.
Goff, F. G., and P. H. Zedler. 1968. Structural gradient analysis of upland forests in the western Great Lakes area. Ecol. Monogr. 38:65-86.
Habeck, J. R., and R. W. Mutch. 1973. Fire-dependent forests in the Northern Rocky Mountains. Quat. Res. 3:408-424.
———, and T. W. Weaver. 1969. A chemosystematic analysis of some hybrid spruce (*Picea*) populations in Montana. Can. J. Bot. 47:1565-1570.
Hett, J. M., and O. L. Loucks. 1976. Age structure models of balsam fir and eastern hemlock. J. Ecol. 64:1029-1044.
Kessell, S. R. 1976. Wildland inventories and fire modelling by gradient analysis in Glacier National Park. Tall Timbers Fire Ecol. Conf. Proc. 14:115-162.
Kilgore, B. M. 1971. The role of fire in managing red fir forests. Trans. North Amer. Wlf. and Nat. Res. Conf. 36:405-416.
———, and D. Taylor. 1979. Fire history of a sequoia-mixed conifer forest. Ecology 60:129-142.
Knight, D. H., and O. L. Loucks. 1969. A quantitative analysis of Wisconsin forest vegetation on the basis of plant function and gross morphology. Ecology 50:219-234.
Lunan, J. S., and J. R. Habeck. 1973. The effects of fire exclusion on ponderosa pine communities in Glacier National Park, Montana. Can. J. For. Res. 3:574-579.
National Oceanic and Atmospheric Administration. 1978. Climates of the States. Volume 1. Gale Research Co., Detroit, Michigan.
Parker, A. J. 1982. Comparative structural/functional features in conifer forests of Yosemite and Glacier National Parks, USA. Amer. Midl. Nat. 107:55-68.
Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest Habitat Types of Montana. U.S. For. Serv., Intermountain For. and Range Exp. Sta., Ogden, Utah.
Peet, R. K., and O. L. Loucks. 1977. A gradient analysis of southern Wisconsin forests. Ecology 58: 485-499.
Rundel, P. W., D. J. Parsons, and D. T. Gordon. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges, pp. 559-599 *in* Terrestrial Vegetation of California. M. G. Barbour and J. Major (eds.). Wiley-Interscience, New York.
Vale, T. R. 1981. Tree invasion of montane meadows in Oregon. Amer. Midl. Nat. 105:61-69.
Vankat, J. L., and J. Major. 1978. Vegetation changes in Sequoia National Park, California. J. Biogeogr. 5:377-402.
Waring, R. H., and J. F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204:1380-1386.
Whipple, S. A., and R. L. Dix. 1979. Age structure and successional dynamics of a Colorado subalpine forest. Amer. Midl. Nat. 101:142-158.
Wright, H. E., Jr. 1974. Landscape development, forest fires, and wilderness management. Science 186:487-495.

Received October 8, 1982
Accepted for publication April 4, 1983

John O. Whitaker, Jr.

Department of Life Sciences
Indiana State University
Terre Haute, Indiana 47809

and

Chris Maser

USDI Bureau of Land Management
Forestry and Sciences Laboratory
3200 Jefferson Way
Corvallis, Oregon 97331

Parasitic mites of voles of the genera Microtus and Clethrionomys from Oregon[1]

Abstract

The more important mites found in the fur of seven species of voles from Oregon were *Laelaps kochi, L. alaskensis, Androlaelaps fahrenholzi,* and *Echinonyssus isabellinus* on *Microtus montanus*; *L. kochi, Haemogamasus occidentalis, Euryparasitus* sp., and *A. fahrenholzi* on *M. oregoni*; *Haemogamasus reidi* and *A. fahrenholzi* on *M. logicaudus*; *H. occidentalis, L. alaskensis,* and *A. fahrenholzi* on *M. richardsoni*; *Euryparasitus* sp., *A. fahrenholzi, Haemogamasus* sp. #2, and *Glycypagus hypudaei* on *Clethroionomys californicus,* and *E. isabellinus, H. reidi,* and *A. fahrenholzi* on *C. gapperi.*

The mite faunas of *Microtus* spp. and those of *Arborimus albipes, A. longicaudus,* and *Lagurus curtatus* were compared. Most of the mite faunas differed considerably from one another. Pairs of hosts having the most similar mite-faunas were *Arborimus albipes-Clethrionomys,* and *M. townsendi-M. montanus.* The most distinctive mite-fauna was that of the red tree vole, *Arborimus longicaudus,* which lives high above ground, primarily in large Douglas-fir trees, *Pseudotsuga menziesii.*

Introduction

During studies of Oregon mammals, long-tailed voles, *Microtus longicaudus*; montane voles, *M. montanus*; creeping voles, *M. oregoni*; Townsend voles, *M. townsendi*; water voles, *M. richardsoni*; California red-backed voles, *Clethrionomys californicus*; and southern red-backed voles, *C. gapperi*, were examined for the presence of mites. The purpose of the study was to determine the species of mites parasitizing these voles. Observations were also made to determine how the composition of mite-faunas correlated with the host-relations, and with host-habitat relationships.

We have previously presented information on the larger mites parasitizing three other species of voles from Oregon: white-footed vole, *Arborimus albipes*; red tree vole, *A. longicaudus*; and sage vole, *Lagarus curtatus* (Whitaker and Maser 1979). The mite found in greatest numbers on all three of these voles was *Androlaelaps fahrenholzi.* Second in number was *Euryparasitus* sp. (not parasitic) on *A. albipes*, and *Glycyphagus hypudaei* on the other two hosts.

[1]The present paper is a partial contribution of the Oregon Coast Ecological Survey, Puget Sound Museum of Natural History, University of Puget Sound, Tacoma, Washington.

TABLE 1. Mites found in the fur of four species of **Microtus** from Oregon.

	Microtus montanus				**Microtus oregoni**				**Microtus townsendi**				**Microtus longicaudus**			
	Infested		No. mites		Infested		No. mites		Infested		No. mites		Infested		No. mites	
	No.	%	Total	x	No.	%	Total	x	No.	%	Total	x	No.	%	Total	x
No. examined	98				76				15				28			
Laelapidae																
Androdaelaps fahrenholzi	59	60.2	317	3.23	8	10.5	20	0.26	8	53.3	21	1.40	8	28.6	102	3.64
Eubrachylaelaps debilis	1	1.0	1	0.01					1	6.7	1	0.07				
Eulaelaps stabularis	2	2.0	4	0.04	1	1.3	3	0.04	2	13.3	2	0.13	1	3.6	1	0.04
Haemogamasus occidentalis	5	5.1	40	0.41	12,	15.8	55	0.72	5	33.3	6	0.40	2	7.1	5	0.18
H. reidi	7	7.1	11	0.11					9	60.1	28	1.87	7	25.0	9	0.32
Haemogamasus sp. ♯2					6	7.9	74	0.97	1	6.7	1	0.07				
Echinonyssus isabellinus	18	18.4	85	0.87					2	13.3	4	0.27				
E. obsoletus									2	13.3	6	0.40				
Hypoaspis miles									2	13.3	3	0.20				
Laelaps alaskensis	53	54.1	351	3.58												
L. kochi	60	61.2	252	2.57	23	30.3	134	1.76	2	13.3	13	0.87	20	71.4	102	3.64
Myobiidae																
Radfordia hylandi					1	1.3	1	0.01								
Glycyphagidae																
Dermacarus hylandi	?1	1.0	6	0.06												
D. ondatrae					1	1.3	1	0.01								
Glycyphagus hypudaei	7	7.1	65	0.66	1	1.3	3	0.04	1	6.7	1	0.07				
Listrophoridae																
Listrophorus mexicanus	1	1.0	34	0.35	1	1.3	50	0.66	1	6.7	1	0.07				
Others																
Cyrtolaelaps sp.	1	1.0	1	0.01									1	3.6	1	0.04
Euryparasitus sp.					10	13.2	15	0.20								
Macrocheles	1	1.0	1	0.01					1	6.7	1	0.07				
Procotolaelaps sp.					1	1.3	1	0.01								
Anoetidae					1	1.3	8	0.11								
Cyrtolaelapid									1	6.7	1	0.07				

Materials and Methods

The voles were caught in museum snap traps. Mites were collected by brushing the voles with a fine-bristled toothbrush, then examining them with a 16-power handlens while blowing the fur. Mites found by the latter method were picked off with forceps. This procedure was satisfactory for the larger mites, but was not so effective for the smaller ones. Mites were preserved in 70-percent ethanol, cleared and stained in Nesbitt's solution containing acid fuchsin, and mounted in Hoyer's solution.

Results and Discussion

Data for five species of *Microtus* and two species of *Clethrionomys* are given in tables 1 and 2 and, for coparative purposes, mites that occurred at rates of 10 percent or more on any one species are listed in order of decreasing abundance (Table 3).

The numbers of species that occurred on 10 percent or more of the samples ranged from two to four (Table 3). (*Listrophorus maxicanus* was omitted from consideration because it appeared that it, along with some of the other small mites, was too often overlooked.) Two of the hosts exist under specialized conditions: (1) *Largurus*, which occurs in areas unusually arid for a vole, was one of the voles least commonly infested by mites (only two species of mites occurred on 10 percent or more of the sample), and (2) *Ariborimus longicaudus*, which occurs high in Douglas-fir (*Pseudotsuga menziesii*) trees, yielded mites of only five species, including a myobiid mite, *Radfordia arborimus*, recently described as a result of these studies (Fain and Whitaker 1975). *Lagurus curtatus* harbored mites of 10 species although only 2 were common. Except for *Microtus longicaudus*, which also had 2 species of commonly occurring mites, the other hosts had 3 or 4, and 4 to 18 total species.

Overall, hosts with more numerous species also had a higher proportion of commonly occurring mites. The average total numbers were 8, 8.8, and 12.3 species of mites on hosts with 2 ($n = 2$), 3 ($n = 4$), and 4 ($n = 4$) commonly occurring mites.

Androlaelaps fahrenholzi was the most abundant parasite on three of the hosts; *Laelaps kochi* on three; and *Haemogamasus reidi*, *H. occidentalis*, *Echinonyssus isabillinus*, and *Haemogamasus* sp. #2 each one one (Table 3).

Androdaelaps fahrenholzi is a widely distributed, abundant species and is found on a wider range of hosts than is any other parasitic mite in North America (Whitaker and Wilson 1974). It may, however, represent a complex of species. *Androlaelaps fahrenholzi* was the only mite found on all 10 voles considered here (Table 3), and occurred at rates greater than 10 percent on voles of all the 10 species considered, ranging from 10.5 percent on *Microtus oregoni* to 88.2 percent on *Arborimus longicaudus*. It was the most common mite on three species of voles, including *Arborimus longicaudus*, *A. albipes*, and *Lagaurus curtatus* (the mean number per host also was high on both species of *Arborimus*; 15.55 and 28.9). *Androlaelaps fahrenholzi* was the second most abundant mite on four hosts—three species of *Microtus* and *Clethrionomys californicus*; fourth most abundant on *Microtus oregoni*, but third on *Clethrionomys gapperi* and *M. richardsoni*. Mean numbers per host ranged from 0.26 on *M. oregoni* to 28.9 on *A. longicaudus*.

Haemogamasus ambulans was previously reported from *Microtus longicaudus* by Whitaker and Maser (1979) and from *Sorex yaquinae* by Whitaker *et al.* (1980). The specimens involved all appeared to be the species of *Haemogamasus* reported here

TABLE 2. Mites found in the fur of **Microtus richardsoni** and two species of **Clethrionomys** from Oregon.

	Clethrionomys californicus Infested No. mites				**Clethrionomys gapperi** Infested No. mites				**Microtus richardsoni** Infested No. mites			
	No.	%	Total	x	No.	%	Total	x	No.	%	Total	x
No. examined	94				8				9			
Laelapidae												
Androlaelaps fahrenholzi	20	21.3	184	1.96	3	37.5	7	0.88	2	22.2	3	0.33
Echinonyssus isabellinus	3	3.2	4	0.04	6	75.0	19	2.38	1	11.1	20	2.22
E. obsoletus	1	1.1	1	0.01								
Eulaelaps stabularis	7	7.4	8	0.09								
Haemogamasus occidentalis	3	9.6	12	0.13					4	44.4	33	3.67
H. reidi	9	9.6	12	0.13	5	62.5	9	1.13	1	11.1	2	0.22
Haemogamasus sp. #2	21	22.4	89	0.95								
Laelaps Alaskensis									4	44.4	16	1.78
Myobiidae												
Protomyobis brevisetosa	1	1.1	1	0.01								
Mycoptidae												
Myocoptes japonensis	1	1.1	1	0.01					1	11.1	1	0.11
Glycyphagidae												
Glycyphagus hypudaei	10	10.6	121	1.29	1	12.5	1	0.13	1	11.1	1	0.11
Listrophoridae												
Listrophorus mexicanus	1	1.1	80	0.85					2	22.2	28	3.11
Others												
Cyrtolaelaps sp.	3	3.2	3	0.03								
Euryparasitus sp.	27	28.7	45	0.48					1	11.1	1	0.11
Macrochelidae	1	1.1	1	0.01								
Bakerdania sp.	1	1.1	7	0.07					2	22.2	2	0.22
Pygmephorus designatus	1	1.1	3	0.03								

as *Haemogamasus* sp. #2. *Haemogamasus ambulans* apparently has not been found in Oregon.

The three species of *Haemogamasus* exhibited much variation in numbers among the 10 voles. *Haemogamasus* sp. #2 was not taken on six of the hosts; had a low prevalence (less than 10 percent infestation) on two, and occurred commonly on only two, *Clethrionomys californicus* and *Arborimus albipes*. *Haemogamasus occidentalis*, a common parasite of western small mammals, occurred on six of the hosts. It was not the predominant mite on any, but was the second most common on *Microtus richardsoni* and *M. oregoni*. It occurred at a high mean number per individual (3.67) on *M. richardsoni*. *Haemogamasus reidi* was not recorded from three of the host species, occurred at a low rate on three, and was common on *Microtus townsend*, *M. richardsoni*, and *Clethrionomys gapperi*. One vole, *Arborimus longicaudus*, had no *Haemogamasus* at all, whereas *Microtus townsendi* and *M. richardsoni* had two (*H. occidentalis* and *H. reidi* in each case). Three species, *Microtus montanus*, *M. longicaudus*, and *Lagurus curtatus*, had zero, one, or two species of *Haemogamasus*, but none occurred at high rates.

Echinonyssus isabellinus occurred on five of the species, commonly on three, *Microtus montanus*, *M. townsendi*, and *Clethrionomys gapperi*.

Laelaps alaskensis and/or *L. kochi* occurred commonly on five species, all *Microtus*. *Laelaps kochi* was found on all the species of *Microtus* except *M. richardsoni* and only on this genus. It had the highest percentage occurrence in three of the species, but was fourth on *M. townsendi*. The mean number per host was rather high in all cases, ranging from 0.87 in *M. townsendi* to 3.64 in *M. longicaudus*. *Laelaps alaskensis*, often common on voles, was first on *Microtus richardsoni*, and third on *M. montanus* and occurred at high rates (both in percent occurrence and means). This species, however, did not occur on any of the other eight vole species.

The one myobiid included as commonly found was *Radfordia arborimus* (Fain and Whitaker 1975), described as a result of these studies.

Glycyphagus hypudaei was the second most widely occurring species, found on nine of the hosts (none was found on *M. longicaudus*Q. It was the second most commonly occurring species on *Arborimus longicaudus* and on *Lagurus*. It occurred at a frequency of 10 percent or more on six of the hosts: *Clethrionomys californicus*, *C. gapperi*, *Microtus richardsoni*, *Arborimus albipes*, *A. longicaudus*, *and Lagurus curtatus*.

Mites of the genus *Euryparasitus* are not parasitic. Nymphs are common on small mammals, but their relationship to the host is not known. *Euryparasitus* (probably more than one species) occurred on six of the voles, and on more than 10 percent of the individuals of four: *Microtus oregoni*, *Clethrionomys californicus*, *Microtus richardsoni*, and *Arborimus albipes*. It was second in occurrence on *Clethrionomys californicus* and *Arborimus albipes*. At least one species of histiostomatid mite occurred on three of the species and at the 10-percent rate on *Microtus richardsoni* and *Arborimus longicaudus*. Histiostomatids are phoretic in the deutonymphal stage on a variety of animal hosts.

Thus, there was some similarity between the host communities, but by no means can it be said that mites moved freely between hosts. If that were the case, mite communities should be similar. As a means of comparing community structure, mites were listed by decreasing percent occurrence for each host (Table 3). No two host species had the same order of occurrence of mites, nor even the same mites in differing order.

As mentioned before, *Arborimus longicaudus* differs the most ecologically from the

TABLE 3. Mites of the 10 species of voles listed in order of decreasing percent occurrence. For each host species, parasite species listed above the line occurred at frequencies greater than 10 percent. (This table includes mites that occurred at rates of 10 percent or more on any one species.)

	Microtus					Clethrionomys		Arborimus		Lagurus
	montanus	**longicaudus**	**oregoni**	**townsendi**	**richardsoni**	**gapperi**	**californicus**	**albipes**	**longicaudus**	**curtatus**
	kochi	kochi	kochi	reidi	alask	isab	**H. sp.**	fahr	fahr	fahr
	fahr	**fahr**	occid	fahr	occid	reidi	Eury	Eury	hypud	**hypud**
	alask	reidi	Eury	**occid**	**fahr**	**fahr**	fahr	H. sp.	anoe	reidi
	isab	Eury	**fahr**	isab	reidi	hypud	**hypud**	**hypud**	**Radf**	isab
	reidi		H. sp.	kochi	hypud		reidi	occid		Eury
	occid		hypud	hypud	Eury		occid			
	hypud		anoe	H. sp.	anoe		isab			
n	98	28	76	15	9	8	94	33	17	**98**
sp.	13	6	13	14	10	4	18	7	5	10
10%	4	2	4	3	3	3	4	3	4	2

Key to abbreviations:

kochi = **Laelaps kochi**
fahr = **Androdaelaps fahrenholzi**
alask = **Laelaps alaskensis**
isab = **Echinonyssus isabellinus**
reidi = **Haemogamasus reidi**
occid = **Haemogamasus occidentalis**
hypud = **Glyceyphagus hypudaei**
Eury = **Euryparasistus** sp.
H. sp. = **Haemogamasus** sp. #2
ano = **anoetid** sp.
Radf = **Radfordia arborimus**
n = No. hosts examined
sp. = Total parasite species found
10% = No. parasites occurring at greater than 10% frequency.

other vole species, a separation reflected in the mite community because only five species of mites were taken. The two most widespread mites, *A. fahrenholzi* and *G. hypudaei*, were the only species that occurred in a relatively large percentage of the individuals.

There was a close relationship of mite communities between *Microtus townsendi* and *M. montanus*. Seven species of mites were found on *M. townsendi* and on *M. montanus*; six of them occurred on both, but *Haemogamasus* sp. #2 occurred only on *M. townsendi* and *Laelaps alaskensis* occurred only on *M. montanus*. The close mite community relationship between *M. townsendi* and *M. montanus* is plausible because both species of voles are constrained by runways and inhabit moist to wet areas, and they share wide-ranging mite species that occur on both sides of the Cascade Range. *Haemogamasus* sp. #2, on the other hand, occurs only west of the Cascade crest, as does its host, *M. townsendi*, and *Laelaps alaskensis* occurs from the crest of the Cascade Range eastward, as does its host, *M. montanus* (Maser and Storm 1970).

A second close mite community relationship was that between *Clethrionomys californicus* and *Arborimus albipes*. Five species occurred on *A. albipes*. The same five species occurred on *C. californucus*, plus two additional species: *Haemogamasus reidi* and *Haemogamasus* sp. #2. Both *C. californicus* and *A. albipes* are largely fossorial and share a similar geographical distribution—south of the Columbia River from the crest of the Cascade Range westward. They are, in fact, sympatric in some areas. That *C. californicus* had two additional mite species is not surprising because this vole has a wider latitude of habitats than does *A. albipes* (Maser *et al.* 1981).

Microtus oregoni and *M. richardsoni* also showed community similarities. Each had seven mites species, five shared. *M. oregoni* is largely fossorial and is not closely tied to aboveground runway systems. *M. richardsoni*, on the other hand, is primarily a semi-aquatic stream dweller of the high Cascades (above 6,000 ft.), and is more rigidly governed by its aboveground runways. These voles are sympatric, however, in some lower elevation areas along the western flank of the Cascades (Maser and Storm 1970).

Clethrionomys gapperi showed similarities with *Lagurus curtatus*. *Clethrionomys gapperi* harbored four species of mites. These four and one additional species were found on *L. curtatus*. Both *C. gapperi* and *L. curtatus* occur east at the Cascade Range and are narrowly allopatric in portions of the Blue Mountains of northeastern Oregon.

The *Microtus longicaudus* mite community differed considerably from other *Microtus* communities. *Microtus longicaudus*, in Oregon, consists of four clearly defined subspecies that essentially represent four different geographical areas (Hall 1981, Maser and Storm 1970). The subspecies, *abditus*, occurs only in northwestern Oregon, west of the Cascade Range. *Microtus longicaudus angusticeps* extends from northwestern California northward into southwestern Oregon, but only along the coast. *Microtus longicaudus* (= *M. longicaudus mordax*) occurs east of the Cascade Mountains, throughout the rangelands of central and southeastern Oregon. Of the four subspecies, *abditus* occupies the wettest areas—primarily riparian areas—and is not dependent on runways. The subspecies, *angusticeps*, inhabits grassy areas and is dependent on aboveground runways. *Microtus longicaudus halli* is essentially a species of grassy riparian areas within the coniferous forest and may or may not be dependent on aboveground runways. The subspecies, *longicaudus* (=*mordax*), occurs from riparian areas in ponderosa pine, *Pinus ponderosa,* forests into dry sagebrush, *Artemisia* spp., regions. This subspecies is not constrained by runways. The mites from *M. longicaudus* came from different subspecies

from widely scattered localities within Oregon which, when coupled with the small sample size (28), may account for lack of similarity with other *Microtus* communities.

Finally, *Arborimus longicaudus* is not only the most specialized vole within the state but also the most widely removed from the other voles (Johnson 1973). The latter is true because it is the only vole that is almost strictly arboreal (Maser *et al.* 1981). Even its cogener, *A. albipes*, is primarily terrestrial (Johnson and Maser 1982, Voth *et al.* 1983). Thus it is not surprising that this community is quite different from others.

The most similar communities were not of the taxonomically most closely related forms. The *Microtus longicaudus* community differed considerably from the other *Microtus* communities. The two species of *Clethrionomys* shared only one major mite species. Mites of *C. californicus* were similar to those of *A. albipes*. The second species of *Arborimus*, *A. longicaudus*, was the most ecologically isolated species of all. This analysis indicates a rather low degree of similarity between these voles' parasite communities, and also relatively little similarity between taxonomically related forms.

Parasitic or phoretic species not previously reported from Oregon are *Hypoaspis miles*, *Dermacarus ondatrae*, and *Myocoptes japonensis*.

New parasitic or phoretic host records are: *Eubrachylaelaps debilis*, *Haemogamasus occidentalis*, *Glycyphagus hypudaei*, *Dermacarus hylandi* (?), and *Listrophorus mexicanus* on *Microtus montanus*; all the records from *Microtus oregoni*, except *A. fahrenholzi*; all records from *Microtus townsendi*, except *Haemogamasus*; *Eulaelaps stabularis* on *Microtus longicaudus*; *Androlaelaps fahrenholzi*, *Haemogamasus occidentalis*, *H. reidi*, *Mycoytes japonensis*, *Glycyphagus hypudaei*, and *Listrophorus mexicanus* from *Microtus richardsoni*; and all records from *Clethrionomys californicus*, except *Echinonyssus obsoletus*.

Although some sense can be made from our analysis of the mite community relationships from the 10 species of voles that we examined, there are some apparent problems with the interpretation of such data. Larger host sample sizes are necessary, particularly in an area as diverse as Oregon because the hosts were collected throughout the State. The communities should be analyzed on the basis of host subspecies, georgraphic distribution, habitat affinities, and physiographic provinces (Franklin and Dyrness 1973, Maser and Storm 1970).

Acknowledgments

We thank Alex Fain (Institut de Medicine Tropicale Prince Leopold, Antwerpen) for identifying some of the smaller mites, and Nixon Wilson (Department of Biology, University of Northern Iowa, Cedar Falls) for examination of some of the *Haemogamasus* and *Echinonyssus*. Gerald Krantz (Department of Entomology, Oregon State University, Corvallis), Donald K. Grayson (Department of Anthropology, University of Washington, Seattle), and Robert L. Rausch (Division of Animal Medicine, School of Medicine, University of Washington, Seattle) critically read and improved the manuscirpt. Phyllis Taylor-Hill (Bureau of Land Management, Forestry Sciences Laboratory, Corvallis, Oregon) typed various drafts of the manscript.

We are grateful for the help.

Literature Cited

Fain, A., and J. O. Whitaker, Jr. 1975. Two new species of Myoiidae from North American mammals (Acarina). Bull. Ann. Soc. r. belge Ent. III: 57-65.

Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, 417 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon

Hall, E. R. 1981 The mammals of North America. Vol. II (sec. ed.). John Wiley & Sons, N. Y. 777-823..

Johnson, M L. 1973. Characters of the heather vole, *Phenacomys*, and the red tree vole, *Arborimus*. J. Mammal. 54: 239-244.

Johnson, M. L., and C. Maser. 1982. Generic relationships of *Phenacomys albipes*. Northw. Sci. 56: 17-19.

Maser, C., and R. M. Storm. 1970. A key to Microtinae of the Pacific Northwest (Oregon, Washington, Idaho). Publ. by O.S.U. Book Stores, Inc, Corvallis, Oregon.

Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981. Natural History of Oregon Coast mammals. USDA For Serv Gen Tech Rep PNW-133, 496 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon.

Voth, E. H., C. Maser, and M. L. Johnson. 1983. Food habits of *Arborimus albipes*, the white footed vole, in Oregon. Northw. Sci. 57: 1-7.

Whitaker, J. O., Jr., and C. Maser. 1979. Parasitic mites of voles of the genera *Arborimus* and *Lagurus* in Oregon. Northw. Sci. 53: 224-227.

Whitaker, J. O., Jr., G. L. Tieben, and C. Maser. 1980. Mites (excluding chiggers) from the fur of five species of western Oregon shrews. Northw. Sci 54: 26-29

Whitaker, J. O., Jr., and N. Wilson. 1974. Host and distribution lists of mites (Acari), parasistic and phoretic, in the hair of wild animals of North America, north of Mexico. Amer. Midl. Nat. 91: 1-67.

Received June 4, 1982
Accepted for publication September 24, 1982

Irven O. Buss

Professor Emeritus, Wildlife Biology
Washington State University
Pullman, Washington 99164

Comments on an Apparent Sharp-Tailed Grouse Movement in Eastern Montana

Abstract

Observations on Sharp-tailed Grouse (*Pedioecetes phasianellus*) in eastern Montana during mid-November 1978 suggested a seasonal, southward movement.

Studies of prairie grouse are meager compared to that of most other gallinaceous species, and information regarding that of Sharp-tailed Grouse (*Pedioecetes phasianellus*) is particularly limited. On 18 and 19 November 1978 my wife and I observed a concentration of Sharp-tailed Grouse associated with high mortality along U.S. highway 12 in eastern Montana. Although we had driven this stretch of highway annually at this time of year for the past decade, this was the first time that we had observed Sharp-tails anywhere along the route.

We first observed road-killed birds, which were assumed to be pheasants, while driving west-bound along the highway near Hettinger, North Dakota. When we saw eight Sharp-tails standing along the roadside about 2.7 km from the Montana border, we recognized that the birds seen earlier might have been Sharp-tails. We then recorded all observations of live and dead birds from that point to Shawmut, Montana, a distance of 463 km.

We saw a total of 138 Sharp-tails, usually in groups of 2-6 birds. One group of 81 birds was first encountered flying in a southward direction 1.6 km west of Baker. We found a total of 18 road-kills, which represents 12 percent of the birds encountered. Additional mortalities were undoubtedly removed by predators. We saw Black-billed Magpies (*Pica pica*), coyotes (*Canis latrans*), Common Ravens (*Corvus corax*), and one Golden Eagle (*Aquila chrysaetos*) along this stretch of highway.

Tracks of Sharp-tails were easily counted in the snow along the roadway. I counted at least 400 sets of tracks, including one concentration made by about 75 birds in Fallon County. A majority of the tracks indicated that the birds were moving to the south. Although these birds may have concentrated along the highway to collect grit or grain spilled from trucks, most of those we saw continued their movement southward after crossing the highway.

There are a number of records of apparent one-way Sharp-tailed Grouse movements (Ammann 1957, Criddle 1935, Edminster 1954, Hamerstrom and Hamerstrom 1951). Snyder (1935) has given a remarkably detailed account of the great 1932 Sharp-tail exodus from the vicinity of James Bay. His map shows that the birds moved southward, some as far as 190 km. He reports that large areas of grouse habitat containing white birch (*Betula papyrifera*) were defoliated by the birch skeletonizer (*Bucculatrix*

canadensisella) prior to this movement. Grange (pers. comm.) suggests wildfires that devastate large areas containing winter forage plants may also induce such migrations.

While there is no way of determining whether these Montana sightings comprise seasonal shifts (Roberts 1936), north-south movements of the usual sort (Johnson 1934), or, mass dispersal like that Snyder (1935) described, the unusual nature of these sightings, their directionality, and the high rate of mortality associated with the movement, suggest that this may have been a one-way migration.

Literature Cited

Ammann, G. A. 1957. The Prairie Grouse of Michigan. Dept. of Conservation, Lansing.

Criddle, N. C. 1935. Some natural factors governing the fluctuations of grouse in Manitoba. Canadian Field-Nat. 44:77-80.

Edminster, F. C. 1954. American Game Birds of Field and Forest. Scribner's, New York.

Hamerstrom, F. N., Jr., and F. Hamerstrom. 1951. Mobility of the sharp-tailed grouse in relation to its ecology and distribution. American Midland-Nat. 46: 174-226.

Johnson, C. E. 1934. Recollections of the prairie chicken and sharp-tailed grouse in northwestern Minnesota. Wilson Bull. 66: 8-17.

Roberts, T. S. 1936. The Birds of Minnesota. Univ. Minnesota Press.

Snyder, L. L. 1935. A Study of the Sharp-tailed Grouse. Contributions Royal Ontario Museum, Zool. 6.

Received February 15, 1982
Accepted for publication March 25, 1982

K. C. Emerson

560 Boulder Drive
Sanibel, Florida 33957

Chris Maser

U.S. Department of the Interior
Bureau of Land Management
Forestry Sciences Laboratory
3200 Jefferson Way
Corvallis, Oregon 97331

and

John O. Whitaker, Jr.

Department of Life Sciences
Indiana State University
Terre Haute, Indiana 47809

Lice (Mallophaga and Anoplura) from Mammals of Oregon[1]

Abstract

An annotated checklist is provided for 19 species of chewing lice (Mallophaga) and 35 species of sucking lice (Anoplura) from wild and domestic mammals of Oregon. The mallophagans are: *Eutrichophilus setosus, Geomydoecus oregonus, G. idahoensis, G. shastensis, G. thomomyus, Neotrichodectes interruptofasciatus, N. minutus, N. osborni, Pitfrufquenia coypus, Stachiella evminea, S. larseni, Trichodectes canis, Tricholopeurus lipeuroides,* and *T. parallelus.* The anoplurans are: *Enderleinellus osborni, E. tamiasciuri, Fahrenholzia pinnata, Haemodipsus setoni, H. lyriocephalus, Hoplopleura acanthopus, H. arboricola, H. hesperomydis, H. onchomydis, H. sciuricola, H. trispinosa, Latagophthirus rauschi, Linognathus setosus, Microphthirus uncinatus, Neohaematopinus citellinus, N. inornatus, N. laeviusculus, N. marmotae, N. neotromae, N. pacificus, N. sciuropteri, N. semifasciatus, Polyplax alaskensis, P. auricularis, P. spinulosa, Solenopotes capillatus,* and *S. ferrisi.* In addition, the following species were found on domestic mammals and humans: (1) Mallophaga—*Bovicola bovis, B. Limbata, B. ovis, Felicola subrostratus, Gyropus ovalis,* and (2) Anophura—*Haematopinus asini, H. eurysternus, H. suis, Linognathus africanus, L. pedalis, L. vitudi, Pediculus humanus* (from humans), *Pthirus pubis* (from humans) and *Polyplax serrata.*

Introduction

Previous information on the lice of mammals from Oregon was presented by Hansen (1964). Hansen found lice as follows (hosts in parentheses): (1) Mallophaga *Geomydoecus thomomyus* (northern pocket gopher, *Thomomys talpoides*), *Strigiphilus ceblebrachys* (deer mouse, *Peromyscus maniculatus*—contaminant or accidental); and (2) Anoplura—*Fahrenholzia pinnata* (Ord kangaroo rat, *Dipodomys ordi*; Great Basin pocket mouse, *Perognathus parvus*), *Hoplopleura acanthopus* (long-tailed vole, *Microtus longicaudus*; montane vole, *M. montanus*; little brown myotis, *Myotis lucifugus*—contaminant or accidental; deer mouse—contaminant or accidental), *H. arboricola, H. erratica,* and *Neohaematopinus pacificus* (chipmunk, *Eutamias* spp.), *Hoplopleura hes-*

[1]This paper is a partial contribution to the Oregon Coast Ecological Survey, Puget Sound Museum of Natural History, University of Puget Sound, Tacoma, Washington 98416.

peromydis (deer mouse), *N. inornatus* (bushy-tailed woodrat, *Neotoma cinerea*; desert woodrat, *N. lepida*); *Polyplax* probably *abscinssa* (*sic*; undoubtedly *abscisa,* which = *alaskensis*), *P. auricularis* (deer mouse; northern water shrew, *Sorex palustris*—contaminant or accidental), *P. spinulosa* (montane vole).

Maser has been collecting ectoparasites for more than 10 years as part of a larger study on mammals of Oregon. Many of the entries in the following checklist have been derived from this study.

Methods and Materials

Lice were collected by direct examination of a host's hair under a dissecting microscope and by brushing the hair over a white porcelain pan. The lice were initially preserved in 70 percent ethanol and subsequently mounted on permanent slides. Identified specimens have been placed in the United States National Museum, Washington, D.C., and in the Puget Sound Museum of Natural History, University of Puget Sound, Tacoma, Washington. Host voucher specimens are either in the Puget Sound Museum or Natural History or in the collection of Donald K. Grayson, Department of Anthropology and Burke Memorial Museum, University of Washington, Seattle.

Nomenclature for mammals primarily follows Hall (1981) and that for lice, primarily follows Ferris (1951), Stojanovich and Pratt (1961), and Emerson (1972).

Annotated Checklist

Mallophaga, Chewing Lice

Bovicola bovis (Linnaeus, 1758).

Host: Domestic cow, *Bos taurus.* **Location:** GRANT CO., Dayville, April 1933, John Day, Jan. 1947. BENTON CO., Corvallis, July 1929, Jan. 1948. **Source:** U.S. National Museum.

Bovicola limbata (Gervais, 1844).

Host: Domestic Angora goat, *Capra hircus.* **Location:** LINN CO., Fairview, Nov. 1947. LINCOLN CO., Jan. 1963. **Source:** U.S. National Museum.

Bovicola ovis (Schrank, 1781).

Host: Domestic sheep, *Ovis aries.* **Location:** BENTON CO., Corvallis, Feb. 1912, Oct. 1948. **Source:** U.S. National Museum.

Eutrichophilus setosus (Giebbl, 1910).

Host: Porcupine, *Erethizon dorsatum.* **Location:** DESCHUTES CO., Sisters, July 1936. **Source:** U.S. National Museum.

Felicola subrostratus (Burmeister, 1938).

Host: Domestic cat, *Felis catus.* **Location:** MULTNOMAH CO., Portland, Nov. 1921. WASHINGTON CO., Forest Grove, May 1933. **Source:** U.S. National Museum.

Geomydoecus oregonus Price and Emerson, 1971.

Host: Camas pocket gopher, *Thomomys bulbivorus.* **Location:** MULTNOMAH CO.; BENTON CO., vicinity of Corvallis, Oct. 1973, May 1974. **Source:** This study. Note: In addition, Price and Emerson (1971) and Price and Hellenthal (1980) reported a number of individuals of

this species, all form this host, which is endemic to western Oregon.

Geomydoecus idahoensis Price and Emerson, 1971.

Host: Townsend pocket gopher, *Thomomys townsendi.* **Location:** MALHEUR CO., in vicinity of Vale, July 1974, April 1975, March 1975, and May 1975. HARNEY CO., near Fields and Malheur Lake, both July 1975. **Source:** This study.

Geomydoecus shastensis Price and Hellenthal, 1980.

Host: Botta pocket gopher, *Thomomys bottae.* **Location:** JACKSON CO., JOSEPHINE CO., CURRY CO. **Source:** Maser *et al.* (1981), Price and Hellenthal (1980).

Geomydoecus thomomys (McGregor, 1917)

Host: Mazama pocket gopher, *Thomomys mazama*; northern pocket gopher, *Thomomys talpoides.* **Location:** Mazama pocketgopher—DESCHUTES CO., vicinity Three Creek Lake (T17S, R9E, S11), July 1969. LINN CO., Big Lake, August 1969. LANE CO., H. J. Andrews Experimental Forest (T15S, R6E, S33), July 1972. Northern pocket gopher—JEFFERSON CO., vicinity Culver, July and Oct. 1969. KLAMATH CO., vicinity Bonanza, May and June 1971, March and Oct. 1972. MALHEUR CO., Pole Creek (T19S, R39E, S31), June 1975. **Source:** This study. **Note:** Price and Emerson (1971) reported this species of louse from both the Mazama and northern pocket gophers from "Oregon."

Gyropus ovalis Burmeister, 1938.

Host: Domestic guinea pig, *Cavia porcellus.* **Location:** MULTNOMAH CO., Portland, July 1939. **Source:** U.S. National Museum.

Neotrichodectes interruptofasciatus (Kellogg and Ferris, 1915).

Host: Badger, *Taxidea taxus.* **Location:** WALLOWA CO., Charolair Road (T2N, R45E, S29), July 1977. **Source:** This study.

Neotrichodectes minutus (Paine, 1912).

Host: Long-tailed weasel, *Mustela frenata.* **Location:** MALHEUR CO., vicinity of Vale, May 1975. **Source:** This study.

Neotrichodectes osborni Keler, 1944.

Host: Spotted skunk, *Spilogale putorius.* **Location:** COOS CO., vicinity of Bandon, July, Oct., and Nov. 1970, Jan., Feb., and Dec. 1971. CURRY CO., Long Ridge Forest Camp (T38S, R12W, S23), Sept. 1970. Vicinity of Port Orford, Dec. 1970; KLAMATH CO., Keno, August 1935. **Source:** This study and U.S. National Museum.

Pitrufquenia coypus Marelli, 1932.

Host: Nutria, *Myocastor coypus.* **Location:** MARION CO., Salem, 1956. **Source:** U.S. National Museum. **Note:** This species of louse is not native to Oregon but was imported from South America with its host, the nutria.

Stachiella erminea Hopkins, 1941.

Host: Short-tailed weasel, *Mustela erminea.* **Location:** LANE CO., 23 mi. SE Vida, April and May 1968, April 1970. **Source:** This study.

Stachiella larseni Emerson, 1962.

Host: Mink, *Mustela vison.* **Location:** LANE CO., 9 mi. N, 1 mi. w

Gardiner, Feb. and March 1972. COOS CO., vicinity of Bandon, August 1970, Feb. and Sept. 1971. **Source:** This study.

Trichodectes canis (deGreer, 1778).

Host: Coyote, *Canis latrans*. **Location:** COOS CO., Dec. 1923. **Source:** U. S. National Museum.

Tricholipeurus lipeuroides (Megnin, 1884).

Host: Mule deer, *Odocoileus hemionus*. **Location:** LINCOLN CO., Alsea; BENTON CO.; LAKE CO.; UNION CO. **Source:** U.S. National Museum.

Tricholipeurus paraellelus (Osborn, 1896)

Host: Mule deer. **Location:** TILLAMOOK CO.; WASHINGTON CO., Forest Grove; DOUGLAS CO.; GRANT CO., Dayville. **Source:** U.S. National Museum.

Anoplura, Sucking Lice

Enderleinellus osborni Kellogg and Ferris, 1915.

Host: Beechey ground squirrel, *Spermophilus beecheyi*. **Location:** LINCOLN CO., Burnt Woods, July 1968. **Source:** U.S. National Museum.

Enderleinellus tamiasciuri Kim, 1966.

Host: Chickaree, *Tamiasciurus douglasi*. **Location:** TILLAMOOK CO., Cascade Head Experimental Forest, August 1971. **Source:** This study.

Fahrenholzia pinnata Kellogg and Ferris, 1915.

Host: Great Basin pocket mouse, *Perognathus parvus*; Ord kangaroo rat, *Dipodomys ordi*; chisel-toothed kangaroo rat, *D. microps*. **Location:** Great Basin pocket mouse—MALHEUR CO., 6.5 mi. SW Whitehorse Ranch (T38S, R39E, S1); 3 mi. NW Road Reservoir (T27S, R43E, S21), both August 1976. Ord kangaroo rat—MALHEUR CO., 5.5 mi. S Vale, March 1975. HARNEY CO., west end Malheur Lake, July 1975. Chisel-toothed kangaroo rat—MALHEUR CO., Sponge Springs (T20S, R43E, S34), May 1975. **Source:** This study. **Note:** Lice on both species of kangaroo rats were found inside the cheek pouches.

Haematopinus asini (Linnaeus, 1758).

Host: Domestic horse, *Equus caballus*. **Location:** MULTNOMAH CO., Portland, April 1937. GRANT CO., Mount Vernon, April 1933. **Source:** U.S. National Museum.

Haematopinus eurysternus Nitzch, 1918.

Host: Domestic cow. **Location:** CROOK CO., Prineville, January 1947. **Source:** U.S. National Museum.

Haematopinus suis (Linnaeus, 1758).

Host: Domestic swine, *Sus scrofa*. **Location:** CLACKAMAS CO., Oregon City, 1911. **Source:** U.S. National Museum.

Haemodipsus lyriocephalus (Burmeister, 1839).

Host: Black-tailed jackrabbit, *Lepus californicus*. **Location:** MORROW CO., Irrigon, May 1932. **Source:** U.S. National Museum.

Haemodipsus setoni Ewing, 1924.

Host: Mountain cottontail, *Sylvilagus nuttalli*; black-tailed jackrabbit. **Location:** Mountain cottontail—MALHEUR CO., Jordan Valley, July 1976. Black-tailed jackrabbitt—GILLIAM CO., Arlington, April 1933; MORROW CO., Irrigon, May 1932. **Source:** This study and U.S. National Museum.

Hoplopleura acanthopus (Burmeister, 1839).

Host: Montane vole, *Microtus montanus*; long-tailed vole, *M. longicaudus*; creeping vole, *M. oregoni*; sage vole, *Lagurus curtatus*. **Location:** Montane vole—DESCHUTES CO., vicinity of Three Creeks Lake, July 1968. JEFFERSON CO., vicinity of Culver, Dec. 1967, April 1968, Dec. 1969. CROOK CO., vicinity of Prineville, Feb. 1968. MALHEUR CO., vicinity of Vale, April, June 1975; Cottonwood Creek (T26S, R38E, S29), Sept. 1976, vicinity of Jordan Valley, July 1976; Mud Springs (T38S, R40E, S29), August 1976; 6 mi. SE Whitehorse Ranch (T37S, R37E, S27), August 1976. Long-tailed vole—DOUGLAS CO., Bum Creek (T20S, R7W, S19), Feb. 1970. MALHEUR CO., Succor Creek State Park, May 1975. Creeping vole—LINN CO., H. J. Andrews Experimental Forest, Sept. 1972. Sage vole—JEFFERSON CO., vicinity of Culver, Nov. 1969, Jan. 1970. HARNEY CO., vicinity of Steens Mountain summit, August 1975. MALHEUR CO., Cottonwood Creek (T26S, R38E, S29), Sept. 1976; Mud Springs, August 1976; 6.5 mi. SE Whitehourse Ranch, August 1976; Jordan Crater Research Natural Area, August 1976. **Source:** This study. **Note:** This species of louse is primarly a parasite of microtine rodents.

Hoplopleura arboricola Kellogg and Ferris, 1915.

Host: Townsend chipmunk, *Eutamias townsendi*; yellow-pine chipmunk, *E. amoenus*; least chipmunk, *E. minimus*. **Location:** Townsend chipmunk —COOS CO., vicinity of Bandon, Sept. and Dec. 1971. LINCOLN CO., Cascade Head Experimental Forest, April 1971. LANE CO., 23 mi. SE Vida, April 1971; H. J. Andrews Experimental Forest, July, August, Sept. 1972. LINN CO., H. J. Andrews Experimental Forest, July, August, Sept. 1972. Yellow-pine chipmunk—UNION CO., Starkey Experimental Forest and Range, Sept. 1975. HARNEY CO., Steens Mountain, July 1975. Least chipmunk—MAHEUR CO., 8.5 mi. WSW Jordan Valley, July 1976. **Source:** This study. **Note:** A total of 861 ($\bar{x} = 3.73$) individuals of this species of louse were taken from 118 of 231 Townsend chipmunks (mostly from the H. J. Andrews Experimental Forest, Lane and Linn counties).

Hoplopleura hesperomydis (Osborn, 1891).

Host: Deer mouse, *Peromyscus maniculatus*. **Location:** COOS CO., vicinity of Bandon, July 1971. UNION CO., Starkey Experimental Forest and Range, Sept. 1975. MALHEUR CO., Jordan Crater Research Natural Area, July 1974; Succor Creek State Park, Mary 1975; Cottonwood Creek (T18S, R42E, S3), August 1975; 8.5 mi. WSW Jordan Valley, July

1976, Antelope Reservoir (T31S, R45E, S33), July 1976; Mud Springs (T38S, R40E, S29), August 1976; 6.5 mi. SE Whitehorse Ranch, August 1976, 3 mi. NW Road Reservoir (T27S, R43E, S21), August 1976. **Source:** This study.

Hoplopleura onychomydis Cook and Beer, 1959.

Host: Northern grasshopper mouse, *Onychomys leucogaster.* **Location:** MALHEUR CO., 6.5 mi. SE Whitehorse Ranch, August 1976. **Source:** This study.

Hoplopleura sciuricola Ferris, 1921.

Host: Western gray squirrel, *Sciurus griseus*; chickaree, *Tamiasciurus douglasi.* **Location:** Western gray squirrel—BENTON CO., Corvallis, August 1971. Chickaree—TILLAMOOK CO., Cascade Head Experimental Forest, August 1971. LINCOLN CO., Newport. BENTON CO., vicinity of Corvallis. **Source:** This study and U.S. National Museum.

Hoplopleura trispinosa (Kellogg and Ferris, 1915).

Host: Northern flying squirrel, *Glaucomys sabrinus.* **Location:** UNION CO., 10 mi. N 6 mi. W La Grande, May 1976; Drumhill Ridge, June 1978; Starkey Experimental Forest and Range, June 1978. UMATILLA CO., Spring Mountain, June 1978. WALLOWA CO., N of Lostine (T3N, R44E, S19), May 1976; Powwatka Ridge, May 1977; Kuhn Ridge, May 1977. **Source:** This study and U.S. National Museum.

Latagophthirus rauschi Kim and Emerson, 1974.

Host: Canadian river otter, *Lutra canadensis.* **Location:** COOS CO., Broadbent, July 1971. **Source:** This study.

Linognathus africanus Kellogg and Paine, 1911.

Host: Domestic goat. **Location:** MULTNOMAH CO., Portland, Nov. 1921. **Source:** U.S. National Museum.

Linognathus pedalis (Osborn, 1896).

Host: Domestic sheep. **Location:** BENTON CO., Corvallis. **Source:** U.S. National Museum.

Linognathus setosus (van Olfers, 1816).

Host: Coyote; domestic dog, *Canis familiaris.* **Location:** Coyote—MALHEUR CO., Soldier Creek (T32S, R45E), Jan. 1976. Domestic dog—MULTNOMAH CO., Portland. GRANT CO., Canyon City, Mount Vernon. **Source:** This study and U.S. National Museum.

Linognathus vituli (Linnaeus, 1758).

Host: Domestic cow. **Location:** BENTON CO., Corvallis. GILLIAM CO., Lonerock. **Source:** U.S. National Museum.

Microphthirus uncinatus (Ferris, 1916).

Host: Northern flying squirrel. **Location:** UNION CO., Starkey Experimental Forest and Range, May 1978. UMATILLA CO., Spring Mountain, May 1978. **Source:** This study.

Neohaematopinus citellinus Ferris, 1942.

Host: Antelope ground squirrel, *Ammospermophilus leucurus.* **Location:**

MALHEUR CO., Dry Creek (T23S, R43E, S27), July 1975. **Source:** This study.

Neohaematopinus inornatus Kellogg and Ferris, 1915.

Host: Bushy-tailed woodrat, *Neotoma cinerea.* **Location:** LINCOLN CO., Cascade Head Experimental Forest, April and August 1971. MALHEUR CO., Cottonwood Creek (T18S, R42E, S3), August 1975; Bogus Lake, July 1976; Jordan Crater Research Natural Area, July 1976. **Source:** This study.

Neohaematopinus laeviusculus (Grube, 1851).

Host: Beechey ground squirrel; Belding ground squirrel, *Spermophilus beldini*; Townsend ground squirrel, *S. townsendi*; Columbian ground squirrel, *S. columbianus*; Washington ground squirrel, *S. washingtoni*; long-tailed weasel. **Location:** Beechey ground squirrel—LINCOLN CO., Burnt Woods, Yachats. BENTON CO., Corvallis. LANE CO., H. J. Andrews Experimental Forest. Belding ground squirrel—KLAMATH CO., vicinity of Bonanza. CROOK CO., Mud Springs Camp, Ochoco Mountains, July 1964. Townsend ground squirrel—KLAMATH CO., Bonanza, 1933, Klamath Falls, 1934. Columbian ground squirrel—UNION CO., Ladd Canyon, March 1979. Washington ground squirrel—MORROW CO., Boardman Bombing Range, May 1978. Long-tailed weasel—MALHEUR CO., 3.5 mi. S Vale, May 1975. (One louse of this species was found on a weasel taken as it hunted in burrows of Townsend ground squirrels.) **Source:** This study and U.S. National Museum.

Neohaematopinus marmotae Ferris, 1923.

Host: Yellow-bellied marmot, *Marmota flaviventris.* **Location:** CROOK CO., Ochoco Mountains. WASCO CO., Antelope. UNION CO., 1.5 mi. SE Ladd Canyon, March 1979. MALHEUR CO., vicinity of Mesa Reservoir (T22S, R41E, S27), May 1975. KLAMATH CO., Dairy, 5 m. E Bonanza, May 1971. **Source:** This study and U.S. National Museum.

Neohaematopinus neotomae Ferris, 1942.

Host: Desert woodrat, *Neotoma lepida.* **Location:** MALHEUR CO., Succor Creek State Park, May 1975. **Source:** This study.
Park, May 1975. **Source:** This study.

Neohaematopinus pacificus Kellogg and Ferris, 1915.

Host: Townsend chipmunk. **Location:** LANE CO. and LINN CO., H. J. Andrews Experimental Forest, July, August, and Sept. 1972. **Source:** This study.

Neohaematopinus sciuropteri (Osborn, 1891).

Host: Northern flying squirrel. **Location:** UMATILLA CO., Spring Mountain (T1S, R36E, S25), May 1978. UNION CO., Starkey Experimental Forest and Range, Sept. 1975, Oct. 1976, May and June 1977, and May and June 1978; 10 mi. N 6 mi. W La Grande, May 1976; 7 mi. N 5 mi. W La Grande, May 1976; Drumhill Ridge, July 1979. WALLOWA CO., Powwatka Ridge, March 1976, March, May, and Dec. 1977, Feb.

1978; 15-17 mi. N Lostine (T3N, R44E, S19), May 1976, Gould Gulch March 1977. **Source:** This study.

Neohaematopinus semifasciatus Ferris, 1916.

Host: Chickaree. **Location:** TILLAMOOK CO., Cascade Head Experimental Forest, August 1971. MULTNOMAH CO., Portlond, March 1951. **Source:** This study and U.S. National Museum.

Pediculus humanus Linnaeus, 1758.

Host: Human, *Homo sapiens*. **Location:** BENTON CO., Corvallis, 1913. **Source:** U.S. National Museum. **Note:** The head louse is the most common human louse in Oregon (Jack Warren, Oregon State Division of Health, Personal comm. 1983).

Pthirus pubis (Linnaeus, 1758).

Host: Human, *Homo sapiens*. **Location:** Oregon. **Source:** Jack Warren (Oregon State Division of Health, personal comm. 1983).

Polyyplax alaskensis Ewing, 1927.

Host: Sage vole.**Location:** JEFFERSON CO., vicinity of Culver, 1969. HARNEY CO., east rim of Steens Mountain, August 1975. **Source:** This study.

Polyplax auricularis Kellogg and Ferris, 1975.

Host: Deer mouse; canyon mouse, *Peromyscus crinitus*. **Location:** Deer mouse—COOS CO., vicinity of Bandon, Nov. 1970, July 1971. MALHEUR CO., Jordan Crater Research Natural Area, July 1974; Succor Creek State Park, May 1975; Antelope Reservoir (10 mi. SW Jordan Valley), July 1976. HARNEY CO., east rim of Steens Mountain, August 1975. Canyon mouse—MALHEUR CO., Succor Creek State Park, May 1975. **Source:** This study.

Polyplax serrata (Burmeister, 1839).

Host: Laboratory mouse, *Mus musculus*. **Location:** BENTON CO., Corvallis, February 1950. **Source:** U.S. National Museum.

Polyplax spinulosa (Burmeister, 1839).

Host: Rat, *Rattus* sp. **Location:** BENTON CO., Corvallis, Nov. 1913. MULTNOMAH CO., Portland, Feb. and March 1934. **Source:** U.S. National Museum.

Solenopotes capillatus Enderlein, 1904.

Host: Domestic cow. **Location:** GRANT CO., John Day, Jan. 1947. **Source:** U.S. National Museum.

Solenopotes ferrisi (Fahrenholz, 1917).

Host: White-tailed deer, *Odocoileus virginianus*. **Location:** BENTON CO. **Source:** Kim and Weisser (1974).

Other species that could occur in Oregon but have not yet been recorded are all Mallophaga: (1) *Bovicola caprae* from short-haired goat; (2) *B. crassipes* from Angora goat; (3) *B. equi* from domestic horse; (4) *B. concavifrons* and *B. longicornis* from North American elk, *Cervus elaphus*; (5) *B. jellisoni* from bighorn sheep, *Ovis canadensis*; (6) *B. oreamnidis* from mountain goat, *Oreamnos americanus*; (7) *Felicola spenceri* from lynx, *Felis lynx*; (8) *Felicola* spp. from cougar, *F. concolor*, and bobcat,

F. rufus; (9) *Heterodoxus spiniger* from domestic dog, *Canis familiaris*, and coyote; (10) *Neotrichodectes mephitidis* from striped skunk, *Mephitis mephitis*; (11) *Stachiella retusa martis* from marten, *Martes americana*; (12) *Suricatoecus quadraticeps* from gray fox, *Urocyon cinereoargenteus*; (13) *Trichodectes octamaculatus* from raccoon, *Procyon lotor*; and (14) *Tricholipeurus pinquis euarctidos* from black bear, *Ursus americanus*.

The only species of louse on a mammal reported by Hansen (1964) but not by us is *Hoplopleura erratica*. Hansen listed it as a probable identification from the chipmunk, *Eutamias* sp. This species of louse, however, seems to be host-specific to the eastern chipmunk, *Tamias striatus*, so we considered it to be an incorrect identification of *H. arboricola*. We took many lice from *Eutamias* but not *H. erratica*. We therefore exclude it from our list of lice on mammals from Oregon.

We have included 19 species of chewing lice and 35 species of sucking lice from wild mammals of Oregon, plus and additional 5 species of chewing lice and 9 species of sucking lice from domestic mammals and humans.

Acknowledgments

Laboratory space and partial funding for this study were provided by the USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Project 1701, Range and Wildlife Habitat Laboratory, La Grande, Oregon. We sincerely appreciate the help of D. K. Grayson (Department of Anthropology and Burke Memorial Museum, University of Washington, Seattle), M. L. Johnson (Puget Sound Museum of Natural History, University of Puget Sound, Tacoma, Washington), and G. Krantz (Departfent of Entomology, Oregon State University, Corvallis), who critically read and improved this paper, and P. Taylor-Hill (U.S. Department of the Interior, Bureau of Land Management, Forestry Sciences Laboratory, Corvallis, Oregon), who typed various drafts of the manuscript.

Literature Cited

Emerson, K. C. 1972. Checklist of the Mallophaga of North America (north of Mexico). Part III. Mammal Host List. Desert Test Center. Dugway, Utah.

Ferris, G. F. 1951. The Sucking Lice. Mem. Pac. Coast Entomol. Soc. Vol. I.

Hall, E. R. 1981. The Mammals of North America. 2nd Ed. Vol. I and II. John Wiley & Sons, New York.

Hansen, C. G. 1964. Ectoparasites of mammals from Oregon. Great Basin Natur. 24:75-81.

Kim, K. C., and C. F. Weisser. 1974. Taxonomy of *Solenopotes* Enderlein, 1904, with redescription of *Linognathus panamensis* Ewing (Linognathidae: Anoplura). Parasitology 69:107-135.

Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dyrness. 1981. Natural History of Oregon Coast Mammals. USDA For. Serv. Gen. Tech. Rep. PNW-133, 496 pp. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Price, R. D., and K. C. Emerson. 1971. A revision of the genus *Geomydoecus* (Mallophaga: Trichodectidae) of the New Word pocket gophers (Rodentia: Geomyidae). J. Med. Entomol. 8: 228-257.

———, and R. A. Hellenthal. 1980. The *Geomydoecus oregonus* complex (Mallophaga: Trichodectidae) of the western United States pocket gophers (Rodentia:Geomyidae). Proc.Entomol. Soc. Wash. 82:25-28.

Stojanovich, C. J., and H. D. Pratt. 1961. Key to the North American sucking lice in the genera *Hoplopleura* and *Neohaematopinus* with descriptions of two species (Anoplura: Hoplopleuridae). J. Parasitol. 47:312-316.

Received September 27, 1982
Accepted for publication March 16, 1983

Association News

Annual Meeting

The 57th Annual Meeting of the Northwest Scientific Association was held March 21-24 at the University of Montana in conjunction with the 44th Annual Meeting of the Montana Academy of Sciences. The meeting included 8 symposia: Fire Effects on Wildlife Habitat, Research Natural Areas: Baseline Monitoring and Management, Recreation Choice Behavior, Degradation of Soil and Water, Can We Afford Wildlife on Federal Lands?, Fred Shafizadeh Memorial Symposium, Limnology of Glacial Lakes, and The Third Predator Symposium.

In addition to the symposia, there were 229 contributed papers in the following sections: Aquatic Sciences, Botany, Chemistry/Physics, Environmental Sciences and Engineering, Forest Science, Applied Forest Science, Geology/Geography, Mathematics/Statistics, Microbiology, Science Education, Social Sciences, Soils, and Zoology. Copies of the program and abstracts are out of print and are no longer available.

Te May Ching from the Farm Crops Department at Oregon State University was named an Honorary Life Member in recognition of her outstanding contribution to northwest science: Research grants totaling $1943 were awarded to: I. R. Gordon, Indiana University; Mark Haley, Humboldt State University; M. M. Hasey, Washington State University; R. E. Herrington, Washington State University; Scott Lunstrom, Humboldt State University, J. E. Ries, Oregon Museum of Science and Industry; M. A. Stern, Oregon State University; D. M. Wood, University of Washington.

The new (or re-elected) officers of the organization are: President, Oscar Sziklai, University of British Columbia; Vice-President, Raymond Soltero, Eastern Washington University; Secretary, Robert L. Carr, Eastern Washington University. The newly elected Trustees are: William H. Emmingham, Oregon State University; George G. Spomer, University of Idaho; Lee E. Eddleman, Oregon State University; M. A. Radwan, U.S. Forest Service; and Hubertus Kohn, Western Washington University.

1985 Annual Meeting

The meeting dates for the 1985 Annual Meeting of the Association at the University of British Columbia are 22-24 May.

Treasurer's Report (1983)

Income	$18,765.56
Expenses	15,891.09
Checking balance, Dec. 31	23.76
Savings balance, Dec. 31	2,850.71
Reserve fund, Dec. 31	4,000.00
Research fund, Dec. 31	11,300.00

Editor's Report (1983)

Thirty-eight papers were published in Volume 57 of *Northwest Science*. Of 54 new manuscripts received, 35 were accepted for publication, 16 rejected, 1 withdrawn, and 2 are still under review.

Northwest Science Index (1973-82)

A cumulative author bibliography and subject index for *Northwest Science* for the years 1973-82 is still available from the Treasurer. Cost per copy:

$5 for individual or institution members;
$10 for nonmembers.

Meetings

WILDLIFE 2000: Modeling Habitat Relationships of Terrestrial Vertebrates will be held 7-11 October 1984 at the Stanford Sierra Camp, Fallen Leaf Lake, California.

For more information, write Wildlife 2000, Local Arrangements, Dept. Forestry and Resource Management, 145 Mulford Hall, Univ. of Calif., Berkeley, Calif. 94720.

50th NORTH AMERICAN WILDLIFE AND NATURAL RESOURCES CONFERENCE will meet 15-20 March 1985 at the Shoreham Hotel, Washington D.C.

COLONIAL WATERBIRD GROUP will meet 4-7 October 1984 at the Sheraton Inn and Conference Center, Ithaca, New York. Local chairman is Donald A. McCrimmon, Cooperative Research Program, Laboratory of Ornitology, Cornell Univ., Ithaca, N.Y. 14850. For information on the scientific program, write William E. Southern, Dept. Biological Sciences, Northern Illinois Univ., DeKalb, Ill. 60015.

Announcement

John Weber is retiring as editor of *Northwest Science*. We are pleased to announce that H. Clare Wiser, Department of Pure and Applied Mathematics, Washington State University 99164-2930, is the interim editor. All editorial correspondence should henceforth be sent to H. C. Wiser.

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian D. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1984 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaueuser Company, Centralia, Washington

1984 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Oregon Institute of Technology, Klamath Falls, Oregon
Oregon State University, Corvallis, Oregon
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
Saint Martin's College, Lacey, Washington
Seattle Central Community College, Seattle, Washington
Seattle Pacific University, Seattle, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State University, Pullman, Washington
Western Oregon State College, Monmouth, Oregon
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1984 Sustaining Individual Members

R. Michael Anthony, Bend, Oregon
Stephen F. Arno, Florence, Montana
Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
Robert L. Carr, Cheney, Washington
Tim W. Clark, Jackson, Wyoming
Richard G. Cline, Missoula, Montana
Susan G. Conrad, Corvalis, Oregon
George W. Douglas, Victoria, British Columbia, Canada
Arlene T. Doyle, Arcata, California
George R. Fahnestock, Seattle, Washington
William R. Funk, Pullman, Washington
Tom Gnojek, Soda Springs Idaho
Gerald H. Haddock, Wheaton, Illinois
Frederick C. Hall, Portland, Oregon
Charles R. Hatch, Moscow, Idaho
Francis R. Herman, Fairbanks, Alaska
Robert J. Jonas, Moscow, Idaho
Barry L. Keller, Pocatello, Idaho
John H. Larsen, Pullman, Washington
Denis P. Lavender, Corvallis, Oregon
Cal E. Meier, College Station, Texas
Emmett B. Moore, Jr., Richland, Washington
Howard R. Panik, Carson City, Nevada
William H. Rickard, Richland, Washington
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Ronald J. Taylor, Bellingham, Washington
Ralph L. Thompson, Berea, Kentucky
David D. Tillson, Salt Lake City, Utah
James M. Thorpe, Corvallis, Oregon
Daniel W. Uresk, Rapid City, South Dakota
Shepard M. Zedeker, Christiansburg, Virginia

Northwest Science

Information for Authors

The pages of *Northwest Science* are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. *Northwest Science* does not publish notes, letters, or bibliographic papers. Short papers are treated the same as longer manuscripts. All submissions are refereed, usually by two reviewers. Papers are also welcome from authors outside of the Pacific Northwest.

At least one of the authors of all papers considered for publication must be a member of the Northwest Scientific Association.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures)*; provide ample margins. Computer printouts are not acceptable. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, double-spaced and not exceeding five percent of the paper, should precede every article. The abstract should recapitulate the major points of the paper and should be suitable for use by abstracting services.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page.

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials*. Consult with the *Council of Biology Editors (CBE) Style Manual*, 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence should be between senior author and the Editor.

Editing—Manuscripts may be edited for grammatical correctness and clarity.

Galley Proofs and Reprints—One set of proofs will be sent to the senior author for correction shortly before publication; proofs should be returned to the Editor within three days of receipt. Senior authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs.

Page Charges—Page charges are currently $60 per printed page. Publication is not contingent upon payment of page charges, as the Association is prepared to assume them for members whose work is unsupported, but even partial payment would be helpful in order that we may continue this policy.

US ISSN 0029 344X

Northwest Science

Non-Profit Org.
BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

Quarterly Publication of the Northwest Scientific Association

H. CLARE WISER
DEPT. OF PURE AND APPLIED MATH.
WASHINGTON STATE UNIV.
PULLMAN WA
99164

Editor John W. Weber Washington State University

Associate Editors

Botany	Robert L. Carr	Eastern Washington University
Chemistry and Physics	Frank L. Curzon	University of British Columbia
Engineering and Mathematics	Gary L. Sheldon	Washington State University
Forestry	Warren P. Clary	U.S. Forest Service
Geology	Franklin F. Foit, Jr.	Washington State University
Social Sciences	Phillip D. Young	University of Oregon
Soils	Robert L. Edmonds	University of Washington
Zoology	Donald R. Johnson	University of Idaho

Papers published in *Northwest Science* are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts,* and *University Microfilms.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.

Volume 58, Number 3

August 1984

Northwest Science

CONTENTS

165 Aquatic Oligochaeta (Naididae) of Washington
Michael E. Smith

171 Relative Abundance of Small Mammals in Four Successional Stages of Spruce-Fir in Idaho
Jerry H. Scrivner and H. Duane Smith

177 Free-swimming Invertebrate Communities of Vernal Pools in Eastern Washington
Robert L. Kulp and Fred W. Rabe

187 Ultimate Loads for Shallow Funicular Concrete Shells
John W. Weber, Kwong-Chi Wu, and Abholhassan Vafai

195 Bryozoan Behavior in Relation to Autocleaning in **Holoporella brunnea** (Hincks)
Matthew H. Dick

208 Vaccinium Membranaceum Berry Production Seven Years After Treatment to Reduce Overstory Tree Canopies
Don Minore

213 New, Rare, and Unusual Algae from Montana
Daniel Wujek and James L. Wee

222 Temperature Characteristics, Animal Heat Storage, and River Diversion Influence on a Monomictic Lake
Thomas J. Loranger and David Brakke

230 Nesting Ecology of Mourning Doves in Fruit Orchards in North-Central Washington
Richard L. Knight, Diwght G. Smith, David M. Gaudet, Albert W. Erickson

237 Selected Avian Systematic Problems in the Northwest: The 1983 A. O. U. Check-list
John T. Ratti

Quarterly Publication of the Northwest Scientific Association

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science*, is open to individuals for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 3000 students or more $40. All other subscribers, $25 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*

H. Clare Wiser
Department of Mathematics
Pullman, Washington 99164-2930
Washington State University

Officers of the Association

President Oscar Sziklai
University of British Columbia
Vancouver, B.C. (1985)*

Vice-President Ray A. Soltero
Eastern Wasington University
Cheney, Washington (1985)

Secretary Robert L. Carr
Eastern Washington University
Cheney, Washington (1984)

Treasurer Steven J. Brunsfeld
College of Forestry, Wildlife, and Range Sciences
University of Idaho
Moscow, Idaho 83843 (1986)

Past President Stephen F. Arno
USDA, Forest Service
Missoula, Montana (1985)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Black
University of British Columbia
Vancouver, British Columbia
(1985)

Lee E. Eddleman
Oregon State University
Corvallis, Oregon (1987)

William H. Emmingham
Oregon State University
Corvallis, Oregon (1987)

Donald Hanley
Washington State University
c/o University of Washington
Seattle, Washington (1986)

Warren Iliff
Washington Park Zoo
Portland, Oregon (1986)

Susan Kephart
Willamette University
Salem, Oregon (1986)

Hubertus Kohn
Western Washington University
Bellingham, Washington (1987)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

M. A. Radwan
U.S. Forest Service
Olympia, Washington (1987)

Steven R. Seavey
Lewis and Clark College
Portland, Oregon (1985)

George G. Spomer
University of Idaho
Moscow, Idaho (1987)

Robert Stockhouse
Pacific University
Forest Grove, Oregon (1986)

Kareen Sturgeon
Linfield College
McMinnville, Oregon (1985)

B. J. Verts
Oregon State University
Corvallis, Oregon (1986)

*Term of office expires in the year given in parentheses.

PUBLISHED QUARTERLY (FEBRUARY, MAY, AUGUST, AND NOVEMBER) BY THE WASHINGTON STATE UNIVERSITY PRESS, PULLMAN, WASHINGTON 99164-5910

Michael E. Smith

Department of Zoology
University of Wisconsin-Milwaukee
Milwaukee, Wisconsin 53201

Aquatic Oligochaeta (Naididae) of Washington

Abstract

Ten species of Naididae are reported from Washington; of these, six have not been previously reported from the state (*Chaetogaster cristallinus*, *Nais behningi*, *Nais pseudobtusa*, *Nais variabilis*, *Stylaria fossularis*, *Stylaria lacustris*). Possible synonymy of *S. fossularis* with *S. lacustris* is suggested from identical or overlapping setal characteristics between the two species, and collection of both species from the same habitats. North American distributional records of Washington specimens are discussed in addition to morphological characteristics of each species. A key to naidids known to occur in the state is included.

Introduction

Few records of naidid oligochaetes have been reported from Washington. Altman (1936) lists five genera and six species as being present in the state. Hiltunen and Klemm (1980) report an additional species bringing the total to seven. During May 1982, Naididae were collected from 11 freshwater localities in western Washington. Ten species were collected; of these, six have not been previously reported from the state.

Methods

Samples were fixed in 10 percent formalin after collection. Worms were dehydrated in an ascending ethanol series, cleared in methyl salicylate, and mounted whole in Permount (Fisher Scientific Co.). Voucher specimens are in the possession of the author.

Species Accounts

Chaetogaster cristallinus Vejdovsky, 1883

Kitsap County: Square Lake, 25 May 1982 (4 specimens).

No dorsal setae present. Prostomium inconspicuous, with a median incision, clearly seen in specimens collected. This incision, located in the middle of the frontal contour of the prostomium has been used by some researchers as a non-failing character for the species (Brinkhurst and Jamieson 1971, Sperber 1948). Other researchers (Elrick 1976, Poddubnaya 1966) have found the median incision to be an unreliable character; also, depending on the orientation of the mounted specimen, the incision can be difficult to see.

Ventral setae in II, 10-11 per bundle, 192-214 μm in length. Posterior setae range from 108-138 μm in length with 6-7 setae per bundle. The setal lengths of II seem to conform better to those given for *Chaetogaster diaphanus* in the literature, while the posterior setal lengths fall within ranges recorded for *C. cristallinus*, albeit at the upper end of the range (Elrick 1976, Sperber 1948).

Also, 7 setae per bundle for posterior setae has not previously been recorded for *C. cristallinus* (Elrick 1976). This poses a problem in assigning the specimens to *C. cristallinus*, although other worms collected and assigned to *C. diaphanus* show distinct differences in number of setae per bundle, have slightly larger maximum setal measurements in II, and show no signs of a median incision in the prostomium. Examination of gut contents in *C. cristallinus* revealed detritus and chydorid cladocerans.

C. cristallinus is known in the Yukon and Northwest Territories, the Great Lakes and eastward (Hiltunen and Klemm 1980), and Colorado (Elrick 1976). The occurrence of this species in Washington extends to the south its known western distribution.

Chaetogaster diaphanus (Gruithuisen 1828)

Kitsap County: Horseshoe Lake, 25 May 1982 (2 specimens); Square Lake, 25 May 1982 (4 specimens). Mason County: Haven Lake, 30 May 1982 (5 specimens).

No dorsal setae present. Prostomium inconspicuous, without a median incision. Setae in II, 8-9 per bundle, and range from 190-232 μm in length. Posterior setae are 8-9 per bundle and are from 104-128 μm in length. All setal measurements fall within previously reported values, as do number of setae (Elrick 1976, Sperber 1948). Gut contents consisted of detritus, diatoms, and chydorid cladocerans.

Distribution of this species is widespread (Brinkhurst 1964, Hiltunen and Klemm 1980) and has been reported from Washington by Altman (1936).

Chaetogaster limnaei limnaei Von Baer, 1827

Kitsap County: Square Lake, 25 May 1982 (2 specimens).

Worms were found epizoic on a physid snail. No dorsal setae present. Setae in II are 9-10 per bundle and are arranged in a semi-circle. Length of setae are from 80-128 μm. Posterior setae are 4-7 per bundle and range from 104-124 μm long. The teeth of the setae are strongly hooked (Gruffydd 1965, Sperber 1948). Setal measurements for Washington specimens are longer than those reported by Gruffydd (1965) in Britain, and by Elrick (1976) in Colorado. No contents were noticed in the gut of the specimens collected.

Distribution of *C. limnaei limnaei* is widespread (Brinkhurst 1964, Hiltunen and Klemm 1980) and this naidid has been reported from Washington by Altman (1936).

Nais behningi Michaelsen, 1923

Kitsap County: Blackjack Creek, 25 May 1982 (1 specimen). Mason County: Mission Creek, 30 May 1982 (3 specimens); Union River, 30 May 1982 (27 specimens).

Eyes present. Purple pigmentation present in the anterior segments. Dorsal setae hairs and needles 1-2 per bundle; needles are simple-pointed. Needles 38-54 μm in length, hairs 180-220 μm long. Hairs are within reported ranges; needles are shorter than reported by Sperber (1948). Ventral setae in II-V, 5-7 per bundle, strongly curved, longer, and thinner than posterior setae; the distal tooth is much longer than the proximal tooth. Ventral setae II-V from

132-148 μm long; Sperber (1948) reports them to be about 120 μm long. Posterior ventrals are 5 per bundle and range from 120-130 μm in length which is again longer than reported by Sperber (1948). Gut contents consisted of detritus and diatoms.

Hundreds of *N. behningi* were collected in the Union River. Densities were extremely high in the top 1 cm of substrate, especially where algae was present. Distribution is widespread (Hiltunen and Klemm 1980) although this is the first report of this species from Washington.

Nais communis Piguet, 1906

Kitsap County: Square Lake, 25 May 1982 (2 specimens). Mason County: Mission Creek, 30 May 1982 (1 specimen); Tahuya River, 30 May 1982 (1 specimen); Haven Lake, 30 May 1982 (1 specimen); pond off Elfendahl Pass Road by Tahuya River land development, 30 May 1982 (1 specimen); Wooten Lake, 30 May 1982 (6 specimens).

Eyes present or absent (2 specimens). Dorsal setae; hairs 1 per bundle, 244-294 μm in length. Needles with diverging teeth, 2 per bundle, and 50-88 μm long. Hair length is longer than in most reported literature (Sperber 1948), although similar to what was found by Harman, *et al.* (1979) for Texas collections. Ventral setae, 4-6 per bundle; those in II-V are essentially the same size and shape as in VI. Length of distal tooth in VI, and posteriad, approximately equal to proximal tooth. Setae are from 76-110 μm in length, which is longer than elsewhere reported. Gut contents were composed entirely of detritus.

Distribution of *N. communis* is widespread (Brinkhurst 1964, Hiltunen and Klemm 1980) and has been reported from Washington by Altman (1936).

Nais pseudobtusa Piguet, 1906

Kitsap County: Square Lake, 25 May 1982 (4 specimens); Wye Lake, 25 May 1982 (2 specimens). Mason County: pond off Elfendahl Pass Road by Tahuya River land development, 30 May 1982 (3 specimens).

Eyes present. Dorsal setae consist of needles and hairs, 1 per bundle. Needles are simple pointed and 46-54 μm in length; hairs are from 150-190 μm long. Both needle and hair lengths are somewhat shorter than previously reported (Sperber 1948). Ventral setae, 3 per bundle; anterior ventrals are from 52-56 μm long; posterior ventrals measure 48-52 μm in length. Ventral setal measurements are also somewhat shorter than reported in the past; those of II-V are straighter and more slender than setae posteriad. Detritus and diatoms were present in the digestive tract.

Distribution of *N. pseudobtusa* is given by Hiltunen and Klemm (1980) to be: Richmond, Virginia; Lincoln Parrish, Louisiana; St. Mary's River, Chippewa County, Michigan; British Columbia, and northwest Canada. This is a new record for Washington and extends the known range of the species to the south of its present western distribution.

Nais variabilis Piguet, 1906

Kitsap County: Long Lake, 25 May 1982 (3 specimens); Square Lake, 25 May 1982 (2 specimens). Mason County: Haven Lake, 30 May 1982 (5 specimens); Wooten Lake, 30 May 1982 (4 specimens).

Eyes present. Dorsal setae consist of 1 needle and hair per bundle. Needles with essentially parallel teeth; length is from 54-60 μm. Hairs are from 150-280 μm long. Ventral setae are 4 per bundle, those of II-V are longer and thinner than setae posteriad. Setae of II-V measure 104-122 μm in length; VI-posteriad measure 88-110 μm long. Distal tooth of ventral setae VI-posteriad are equal to or slightly shorter than proximal tooth. All setal measurements and numbers are within known ranges. Detritus and diatoms were present within the digestive tract.

Distribution of *N. variabilis* is widespread (Hiltunen and Klemm 1980). No previous record of this species exists from Washington, although it is perhaps the most common of all naidid oligochaetes.

Pristina leidyi Smith, 1896

Kitsap County: Square Lake, 25 May 1982 (2 specimens). Mason County: Wooten Lake, 30 May 1982 (1 specimen).

No eyes. Prostomium elongated into a proboscis. Dorsal setae beginning in II. Serrations are present on all hair setae except those in II and III; hairs of III greatly elongated. Hairs, 2-3 per bundle; measurements of II are approximately 500 μm, those posteriad range from 262-390 μm. Needles are finely bifid, 2-3 per bundle and range from 38-48 μm. Ventral setae are 5-6 per bundle in II, and 38-48 μm long. Ventrals of posterior are 6-7 per bundle and approximately 50 μm in length. All numbers and measurements of setae are within ranges of North American records (Harman and McMahan 1975). Detritus and diatoms were present in the digestive tract.

Distribution of *P. leidyi* is widespread (Hiltunen and Klemm 1980), and Altman (1936) has reported this species as occurring in Washington.

Stylaria fossularis Leidy, 1852

Kitsap County: Long Lake, 25 May 1982 (8 specimens). Mason County: Haven Lake, 30 May 1982 (6 specimens).

Eyes present. Proboscis projecting from the tip of the pointed prostomium. Dorsal setae begin on VI; consist of 1 hair and 1-2 needles per bundle. Needles are from 60-92 μm in length; hairs are serrated and range from 278-440 μm long. Needles are longer and hairs are shorter than has been reported by Sperber (1948). The digestive tract contained detritus and diatoms.

S. fossularis has been considered a *species inquirenda* by Brinkhurst (Brinkhurst 1964, Brinkhurst and Jamieson 1971), who considers it a synonym of *Stylaria lacustris* (Linnaeus 1767). Distribution of *S. fossularis* includes the Great Lakes and Wisconsin to Louisiana, Alabama, South Carolina, West Virginia, and Maine (Hiltunen and Klemm 1980). This species has also been reported from Pennsylvania, Michigan, Tennessee, and (?) Ohio (Brinkhurst 1964). The presence of *S. fossularis* in Washington greatly extends its range to the west; it was heretofore unreported from the state.

Stylaria lacustris Linnaeus, 1767

Kitsap County: Long Lake, 25 May 1982 (2 specimens).

Eyes present. Prostomium elongated into a proboscis which projects from a notch between two lateral lobes. Dorsal setae begin in VI, and consist of 1 hair

and 1-2 needles per bundle. Hairs are 377-560 μm long, finely serrated. Needles are 60-68 μm in length. Ventral setae are 4-6 per bundle, and from 127-158 μm long. Lengths of all setae are somewhat shorter than have been reported in past literature. Gut contents consisted of detritus and diatoms.

Distribution is widespread for *S. lacustris* (Brinkhurst 1964, Hiltunen and Klemm 1980), although it has not been previously reported from Washington.

Numbers of setae are identical between collected specimens of *S. fossularis* and *S. Lacustris*; ranges for setal measurements overlap. *S. Lacustris* does seem to have longer hairs than *S. fossularis*, this being the only noticeable difference. Both species were collected in the same lake and from the same habitats. These factors seem to provide further support for the possible merging of the two species, although evidence provided by collections in this study are certainly not conclusive. Further investigations must be carried out to resolve this question.

Literature Cited

Altman, L. C. 1936. Oligochaeta of Washington. Univ. Wash. Publ. Biol. 4:1-137.

Brinkhurst, R. O. 1964. Studies on the North American aquatic Oligochaeta I: Naididae and Opistocystidae. Proc. Acad. Nat. Sci. Phila. 116:195-230.

———, and B. G. M. Jamieson. 1971. Aquatic Oligochaeta of the World. Univ. Toronto Press.

Elrick, D. L. 1976. The morphology, reproduction, and ecology of Colorado species of *Chaetogaster* (Oligochaeta, Annelida). PhD Thesis. Univ. Colorado, Boulder.

Gruffydd, L. D. 1965. Evidence for the existence of a new subspecies of *Chaetogaster limnaei* (Oligochaeta), in Britain. J. Zool. 146:175-196.

Harman, W. J., and M. L. McMahan. 1975. A reevaluation of *Pristina longiseta* (Oligochaeta: Naididae) in North America. Proc. Biol. Soc. Wash. 88:167-178.

———, M. S. Loden, and J. R. Davis. 1979. Aquatic Oligochaeta new to North America with some further records of species from Texas. Southwest. Nat. 24:509-525.

Hiltunen, J. K., and D. J. Klemm. 1980. A Guide to the Naididae (Annelida: Clitellata: Oligochaeta) of North America. EPA-600/4-80-031, Cincinnati, Ohio.

Poddubnaya, T. L. 1966. On the classification of *Chaetogaster diaphanus* Gruith. (Oligochaeta, Naididae) [in Russian]. Tr. Akad. Nauk. SSR Inst. biol. Vnutr. Vod. 12:120-124.

Sperber, C. 1948. A taxonomical study of the Naididae. Zool. Bidr. Uppsala. 28:1-296.

Received October 4, 1982
Accepted for publication January 7, 1983

Key to the Naididae of Washington

1	Dorsal setae present	4
	Dorsal setae absent	*Chaetogaster* 2
2(1)	Teeth of setae strongly hooked. Epizoic on molluscs	*Chaetogaster limnaei limnaei*
	Teeth of setae not strongly hooked	3
3(2)	Median incision in prostomium	*Chaetogaster cristallinus*
	Without median incision in prostomium	*Chaetogaster diaphanus*
4(1)	Segment II with hair setae	*Pristina* 5
	Segment II without hair setae	6
5(4)	Proboscis present	*Pristina leidyi*
	No proboscis	*Pristina idrensis*[a]
6(4)	Proboscis present	*Stylaria* 7
	No proboscis	8
7(6)	Proboscis arises from a notch in the prostomium between two lateral lobes	*Stylaria lacustris*
	Proboscis arises from the tip of a pointed prostomium	*Stylaria fossularis*
8(6)	Posterior end modified to form caudal gills	*Dero obtusa*[b]
	Posterior end without gills	9

9(8)	More than 3 hair setae per bundle	*Vejdovskyella* sp. [b,c]
	Less than 3 hair setae per bundle	*Nais* 10
10(9)	Needle setae simple-pointed	11
	Needle setae bifid	12
11(10)	Ventral setae of II-V extremely reduced in thickness with long thin teeth, the distal tooth very long, the proximal tooth half as long or less	*Nais behningi*
	Ventral setae of II-V not extremely reduced in thickness with shorter teeth, at a greater angle to each other	*Nais pseudobtusa*
12(10)	Size and shape of ventral setae in VI are essentially the same as in II-V; teeth of needle setae divergent	*Nais communis*
	Size and shape of ventral setae in VI are dissimilar to those in II-V; teeth of needle setae not divergent	*Nais variabilis*

[a]Reported as being collected from King County, Cedar River by Hiltunen and Klemm (1980)—not collected in this study.
[b]Reported by Altman (1936) as present in Washington—not collected in this study.
[c]No species identification was made by Altman (1936).

Jerry H. Scrivner

Department of Wildlife and Fisheries Sciences
Texas A&M University
College Station, Texas 77843

and

H. Duane Smith

Department of Zoology
Brigham Young University
Provo, Utah 84602

Relative Abundance of Small Mammals in Four Successional Stages of Spruce-Fir Forest in Idaho

Abstract

This paper discusses the relative abundance of four small mammal species in successional stages (1-10, 11-39, 40-79, and 80+ years following disturbance) of spruce-fir forest in Idaho. Species evaluated include *Peromyscus maniculatus*, *Eutamius ruficaudus*, *Zapus princeps*, and *Clethrionomys gapperi*. For the specific study sites we investigated, intraspecific comparisons indicated *P. maniculatus* increased with succession; *E. ruficaudus* abundance varied but was generally most common in mid-successional stages; *Z. princeps* preferred willow-alder thickets within mid-successional stages; and *C. gapperi* was most abundant in the mature forest.

Introduction

In many parts of the Pacific Northwest, the logging industry is the dominant land management activity. Thomas *et al.* (1976) pointed out that the weakest link in the process of contrasting alternatives for long term management of forests, was the inability to predict effects on wildlife populations. Since timber management influences wildlife, data on species and population sizes from different forest types, using different forest management procedures are necessary to achieve the needed predictability.

Tevis (1956), Gashwiler (1959, 1970), Hooven and Black (1976), Ahlgren (1966), Stock (1976). and Ramirez and Hornocker (1981) have compared small mammal populations of forested areas with recently logged areas. Less is known, however, about small mammal abundance in relations to forest succession, particularly in the spruce-fir (*Abies* spp.-*Picea* spp.) complex (Hooven 1969). The objective of this study was to investigate the relative abundance of small mammal species in successional stages of spruce-fir forest.

Study Area and Methods

Study areas were located within the Pierce Ranger District of the Clearwater National Forest in Idaho. USDA-Forest Service records of known-aged timber stands were consulted and study sites within two areas (I and II) were selected, successionally representing a range from clear-cut to climax in the spruce-fir association. In each area, one stand of each age class (1-10, 11-39, 40-79, and 80+ years following disturbance) was selected.

Study sites were from 708 to 1539 m above sea level. On the 1-10-year-old sites, Fireweed (*Epilobium agustifolium*), was the dominant forb, with Elderberry (*Sambucus* spp.) and Snowbrush (*Ceanothus velutinus*) the dominant shrubs. In the 11-39 and the 40-79-year-old sites, Heart-leaved Arnica (*Arnica codifolia*) and Twin-flower (*Linnea borealis*) were dominant forbs, and Scouler Willow (*Salix scouleriana*) and Honeysuckle (*Lonicera utahensis*) were dominant shrubs in the 11-39-year-old sites. The dominant shrub in the 40-79-year-old sites was Huckleberry (*Vaccinium membranaceum*). Wild Ginger (*Asareum caudatum*) was the dominant forb in the 80+-year-old sites and Huckleberry (*V. membranaceum*) the dominant shrub. In all successional stages, Grand Fir (*Abies grandis*) was the dominant tree species.

Each of the eight study sites contained one small mammal trapping grid measuring 100 by 100 m (1 ha) with permanently marked trap stations at 10-m intervals. Two Sherman traps, baited with rolled oats, were placed at each trap station. In each of the two areas, approximately two weeks were spent trapping the four study sites. Each grid was trapped for seven consecutive days during August of 1978 and 1979. Grids were checked in morning, afternoon, and evening. Traps containing animals were reset immediately. Data recorded for animals included species, age class, sex, trap location, reproductive condition, and weight. Each animal was toe-clipped for identification then released.

Using a GSK statistical analyses described by Grizzle *et al.* (1969), an X^2 test was used to compare the proportions of animals caught in various stages of succession. For each species, we first tested the null hypothesis that the three main effects (stand age, area, and year) were independent. Since in all instances the three-way test for independence, was significant ($P < 0.05$), we then tested two effects for independence, with the remaining effect fixed at a given level. Generally, the stand age by year within a given area test for independence was nonsignificant ($P > 0.05$); we therefore combined the data for each year within a given area. Thus, because there appeared to be some heterogeneity between area I and II, mammal abundance trends within the four successional stages were analyzed separately for each area, with year treated as replicate.

Results and Discussion

Four species were captured in sufficient numbers during both years for analysis of relative abundance trends (Table 1). These include deer mice (*Peromyscus maniculatus*), red-tailed chipmunks (*Eutamius ruficaudus*), western jumping mice (*Zapus princeps*), and red-backed voles (*Clethrionmys gapperi*). With few exceptions, more individuals of all four species were captured in each successional stage in 1979.

In area I there was an increase in the total number of animals captured as the years since clear-cutting increased. Deer mice were the major contributors to this abundance trend. In area II this trend was not as apparent primarily because of the relatively high number of animals captured in the 1-10-year-old successional stage. Although in a different forest type, Pearson (1959) also found the relative abundance of the total small mammal fauna generally to increase from early seral stages to mature oak forests. He noted that between the 16- and 46-year-old stages, grassland degenerated and the small mammal population decreased abrubtly in abundance. When the forest matured, mammal abundance increased.

On the sites we investigated, the abundance of deer mice generally increased as

TABLE 1. Number of animals captured (1400 trap nights/successional stage/year) within two areas of the Clearwater National Forest in Idaho. Each area contained four study sites, successionally representing a range from clear-cut to mature forest. Data were gathered in August 1978 and 1979.

		Years since clear cutting							
		Area I				Area II			
		1-10	11-39	40-79	80+	1-10	11-39	40-79	80+
1978	**Eutamius ruficaudus**	0	18	28	6	12	11	27	12
	Peromyscus maniculatus	20	11	22	54	14	8	9	19
	Zapus princeps	12	18	21	12	3	0	0	3
	Clethrionomys gapperi	0	1	14	14	1	2	0	6
	Total	32	48	85	86	30	21	36	40
1979	**Eutamius ruficaudus**	7	33	42	7	40	18	14	18
	Peromyscus maniculatus	42	68	69	127	42	31	44	84
	Zapus princeps	9	24	25	22	5	1	0	1
	Clethrionomys gapperi	5	4	34	27	0	4	3	4
	Total	63	129	170	183	87	54	61	107

succession proceeded to climax. In both areas, significantly ($P < 0.05$) more deer mice were captured in the 80+-year-old successional stage than in the 1-10-year-old successional stage. Other authors (Hooven 1969, 1973; Hooven and Black 1976; Stock 1976; Martell and Radvanyi 1977; Ramirez and Hornocker 1981) suggested that early seral stages are most attractive to deer mice, while Harris (1968) and Petticrew and Sadlier (1974) reported little difference in population densities between successional stages.

We were surpised to find deer mice more abundant in the oldest successional stages and suggest additional comparisons should be done, including determination of factors that might influence the distribution of deer mice in spruce-fir forests. Factors thought to influence the distribution of deer mice include food and cover (Hooven and Black 1976, Martell and Radvanyi 1977, Ramirez and Hornocker 1981); intraspecific behavioral interactions and predators (Stock 1976, Sullivan 1979); and long term evolutionary selection (Hooper 1942, Foster 1959).

We then compared the total number of red-tailed chipmunks captured in mid-successional stages (11-39 plus 40-79-year-old sites) with the total number caught in early and late successional stages. In area I, there were significantly ($P < 0.05$) more chipmunks in midsuccessional stages than in the early and late successional stages for both 1978 and 1979. The relatively high chipmunk abundance for mid-successional stages may be related to possible preferences for Alder (*Alnus* spp.) thickets (Hoffman 1960). Such thickets were particularly common in mid-seral stages within area I. In area II, this trend was also evident for 1978; however, in 1979, more chipmunks were caught in early and late successional stages than in mid-successional stages. This phenomenon was primarily due to the over three-fold increase in the number of chipmunks caught in the 1-10-year-old sites.

In general, little is known regarding the effects of logging on red-tailed chipmunks. More has been reported on the congeneric Townsend chipmunk (*Eutamius townsendii*) (Gashwiler 1959, 1970; Ahlgren 1966; Hooven and Black 1976). Generally, chipmunks prefer timber and shrubby-brush areas (Tevis 1956; Hooven and Black 1976). Following cutting, population densities were reported to decline; but three to ten years later,

densities were two to four times greater than virgin forests (Tevis 1956; Gashwiler 1959, 1970).

Few chipmunks were captured in the mature forest. Possibly the presence of the red squirrel (*Tamiasciurus hudsonicus*) has an influence on chipmunk distribution. Broadbooks (1970a) observed pine squirrels (*Tamiasciurus douglasi*) chasing yellow pine chipmunks (*Eutamius amoenus*) from the vicinity of squirrel food caches. Elsewhere, however, Broadbooks (1970b) suggests that whereas the two sciurids may overlap in food and habitat, competition is reduced by each specializing in certain plant foods—the pine squirrel in fresh pine and fir cones, and the chipmunk in seeds and flowering plants.

For both years, we found western jumping mice significantly ($P < 0.05$) more common in the mid-successional stages of area I. These mid-successional stages contained the greatest concentration of Willow (*Salix* spp.)-Alder thickets, reportedly a preferred habitat type (Hoffman 1960; Whitaker 1963; Brown 1967). In area II, jumping mice were more common in the early and late successional stages. In this area, however, the sample size was small in all successional stages, and the results from this group of successional stages are inconclusive, as were most of the references we consulted on *Zapus* and forest succession (Rickard 1960; Gashwiler 1970; Hooven and Black 1976; Ramirez and Hornocker 1981). It is noteworthy that Willow-Alder thickets were not as common in the area II sites as they were in area I.

Though a few investigators (Brown 1967; Clark 1971) have studied preferences of jumping mice for different habitat types, studies in all successional stages are lacking. In comparing the relative abundance of jumping mice in cut and uncut forests, Stock (1976) found jumping mice to be more closely correlated with the local availability of suitable habitat than with overall cover density. He found suitable habitat occurred on both cut and uncut sites. Jumping mice are generally considered inhabitants of grass-bordered streams and meadows (Davis 1934; Hamilton 1935; Whitaker 1963; Stock 1976). Hoffman (1960) and Brown (1967) captured them in moist aspen groves, willow-alder thickets, and damp forb-sedge meadows. Getz (1961) found meadow jumping mice (*Zapus hudsonius*) also inhabiting moist situations and suggested that the type of vegetation did not influence the local distribution. Whitaker (1963), however, believed soil moisture had no effect on jumping mice, except indirectly as it influenced vegetation. Our results generally concur with the view that jumping mice are most common in forest stages containing willow-alder thickets.

When the number of captures of red-backed voles for the 40-70 and 80+-year-old sites are grouped and compared with the number of voles captured in the 1-10 and 11-39-year-old sites, significantly more ($P < 0.05$) animals were found in the oldest two successional stages. Most consider red-backed voles to prefer cool, damp, virgin forests (Tevis 1956; Hoffman 1960; Rickard 1960; Morris 1969; Stock 1976; Ramirez and Hornocker 1981). Stock (1976) found that while red-backed voles favor habitat providing dense overstory, the voles did not necessarily prefer a high percentage of ground cover. He often found clearcut sites to contain high percentages of ground cover. He often found clearcut sites to contain as much or more ground cover as forests, yet clearcut sites still did not produce any voles. Hooven and Black (1976) showed that removal of timber and reduction of vegetative cover reduced habitat suitability. Others may be removed, enough slash debris remain to provide a closed canopy at ground level suggest that logging does not affect red-backed voles, and that even though the canopy

(Tevis 1966; Gashwiler 1959; Ahlgren 1966). When management plans call for logging and slash burning, the habitat is significantly reduced to cause a decline in population level. Whereas Ahlgren (1966) reported population levels began to achieve pre-logging levels three years following cutting and burning, in our study this did not occur until approximately 40 years.

Acknowlegments

This research was funded in part by the U.S./Canada Spruce Budworm Program (USDA-Forest Service). We thank Josh Baker for assisting with the statistical analyses. We appreciate the comments of Samuel L. Beasom, Curtis H. Halvorson, and an anonymous referee for reviewing an earlier draft of this manuscript.

Literature Cited

Ahlgren, C. E. 1966. Small mammals and reforestation following prescribed burning. J. Forestry 64:614-618.

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus*. J. Mamm. 51:310-326.

———. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus*. Amer. Midland Nat. 83:472-488.

Brown, L. N. 1967. Seasonal activity patterns and breeding of the western jumping mouse (*Zapus princeps*) in Wyoming. Amer. Midland Nat. 78:460-470.

Clark, D. H. 1971. Ecology of the western jumping mouse in Grand Teton National Park, Wyoming. Northw. Sci. 45:229-238.

Davis, W. B. 1934. A study of the Idaho jumping mice of the genus *Zapus* with remarks on a few specimens from British Columbia. J. Mamm. 15:221-227.

Foster, D. D. 1959. Differences in behavior and temperament between two races of deer mice. J. Mamm. 40:496-513.

Gashwiler, J. S. 1959. Small mammal study in west-central Oregon. J. Mamm. 40:128-139.

———. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51:1018-1026.

Getz, L. L. 1961. Notes on the local distribution of *Peromyscus leucopus* and *Zapus hudsonius*. Amer. Midland Nat. 65:486-500.

Grizzle, J. E., C. F. Starmer, and G. G. Koch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Hamilton, W. J. 1935. Habits of jumping mice. Amer. Midland Nat. 16:187-200.

Harris, A. S. 1968. Small mammal and reforestation in southwest Alaska. U.S. Forest Serv. Pacific Range Exp. Sta. Res. Note PNW-75.

Hoffman, G. R. 1960. The small mammal components of six climax plant associations in eastern Washington and northern Idaho. Ecology 41:571-572.

Hooper, E. T. 1942. An effect on the *Peromyscus maniculatus* Rassenkries of land utilization in Michigan. J. Mamm. 23:193-196.

Hooven, E. F. 1969. The influence of forest succession on populations of small mammals in western Oregon. Pp. 30-34, *in* Wildlife and Reforestration in the Pacific Northwest (H. C. Black, ed.). Oregon State Univ., Corvalis.

———. 1973. Effects of vegetation changes on small forest mammals. Pp. 75-97, *in* Even-aged Management. (R. K. Hermann, and D. P. Lavender, eds.). Oregon State Univ., Corvalis.

Hooven, E. F., and H. C. Black. 1976. Effects of some clearcutting practices on small mammal populations in western Oregon. Northw. Sci. 50:189-208.

Martell, A. M., and A. Radvanyi. 1977. Changes in small mammal populations after clearcutting of northern Ontario black spruce forest. Canadian Field-Nat. 91:41-46.

Morris, R. D. 1969. Competitive exclusion between *Microtus* and *Clethrionomys* in the aspen parkland of Saskatchewan. J. Mamm. 50:291-301.

Pearson, F. G. 1969. Small mammals and old field succession on the Piedmont of New Jersey. Ecology 40:249-255.

Petticrew, B. G., and R. M. F. S. Sadlier. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. I. Population dynamics. Canadian J. Zool. 52:107-118.

Ramirez, P., and M. Hornocker. 1981. Small mammal populations in different aged clearcuts in norwestern Montana. J. Mamm. 62:400-403.

Rickard, W. H. 1960. Distribution of small mammals in relation to the climax vegetation mosaic in eastern Washington and northern Idaho. Ecology 41:571-572.

Stock, M. K. 1976. Successful Changes in Small Mammal Species Diversity on Clearcuts in the Grand Fir Forest of Northern Idaho. M.S. Thesis. Univ. of Idaho, Moscow.

Sullivan, T. P. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. Canadian J. Zool. 57:1636-1648.
Tevis, L., Jr. 1956. Responses of small mammal populations to logging of Douglas-fir. J. Mamm. 37:189-196.
Thomas, J. W., R. S. Miller, H. Black, J. E. Rodiek, and C. Maser. 1976. Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue mountains of Oregon. Trans. North Amer. Wildl. Conf., 452-476.
Whitaker, J. O. 1963. A study of the jumping mouse, *Zapus hudsonius* (Zimmerman), in central New York. Ecol. Monogr. 33:215-254.

Received December 6, 1982
Accepted for publication April 4, 1983

Robert L. Kulp

and

Fred W. Rabe

Department of Biological Sciences
University of Idaho
Moscow, Idaho 83843

Free-Swimming Invertebrate Communities of Vernal Pools in Eastern Washington

Abstract

Free-swimming invertebrates which consisted mostly of crustaceans and insects were collected weekly from five vernal pools in eastern Washington from 20 February through 18 June 1982. By use of activity traps and a modified Wilding sampler, the planktonic or benthic habit of these taxa were determined. Community composition is compared to a nearby permanent lake and a model of the habit and trophic relationships in the pools is proposed.

Introducton

Vernal pools are temporary bodies of water that form in late winter or early spring from rain and melting snow (Wiggins 1973). Duration of the wet phase varies, but these pools usually dry up in summer (Hartland-Rowe 1972).

Typical invertebrate communities found in vernal pools include phyllopods, copepods, cladocerans, rotifers and dipterans (Hartland-Rowe 1966, Stout 1964, Kenk 1949, Wiggins *et al.* 1980, Simpson 1967, Donald 1971, Fairbanks 1950). Certain taxonomic groups such as Anostraca, Conchostraca, and Notostraca are found primarily in temporary waters (Pennak 1978, Wiggins *et al.* 1980).

The objective of this study was to document the free swimming invertebrate community of five vernal pools and to describe habits and trophic relationships.

Study Area Description

The study site is located 2.5 km south of Cheney, Washington on the Turnbull Pine Research Natural Area (Fig. 1). The site is 81 hectares in area and is part of the Turnbull National Wildlife Refuge, Spokane County, Washington (Franklin *et al.* 1972). The refuge is part of the "channeled scablands" first described by Bretz (1923). Prior to the formation of the scablands, the region was comprised of Columbia River basalt overlain with thick deposits of loess. The scablands are the result of scouring by glacial rivers which left a series of coulees, lakes and marshes which are oriented in a northeast-southeast direction.

The natural area is characterized by various ponderosa pine (*Pinus ponderosa* Douglas) habitat types (Daubenmire 1968). Snowberry (*Symphoricarpos albis* (L.) Blake) is a common understory species. Various grassland communities are also found on the study site (Franklin *et al.* 1972).

All pools studied were surrounded by stands of ponderosa pine and contain quaking

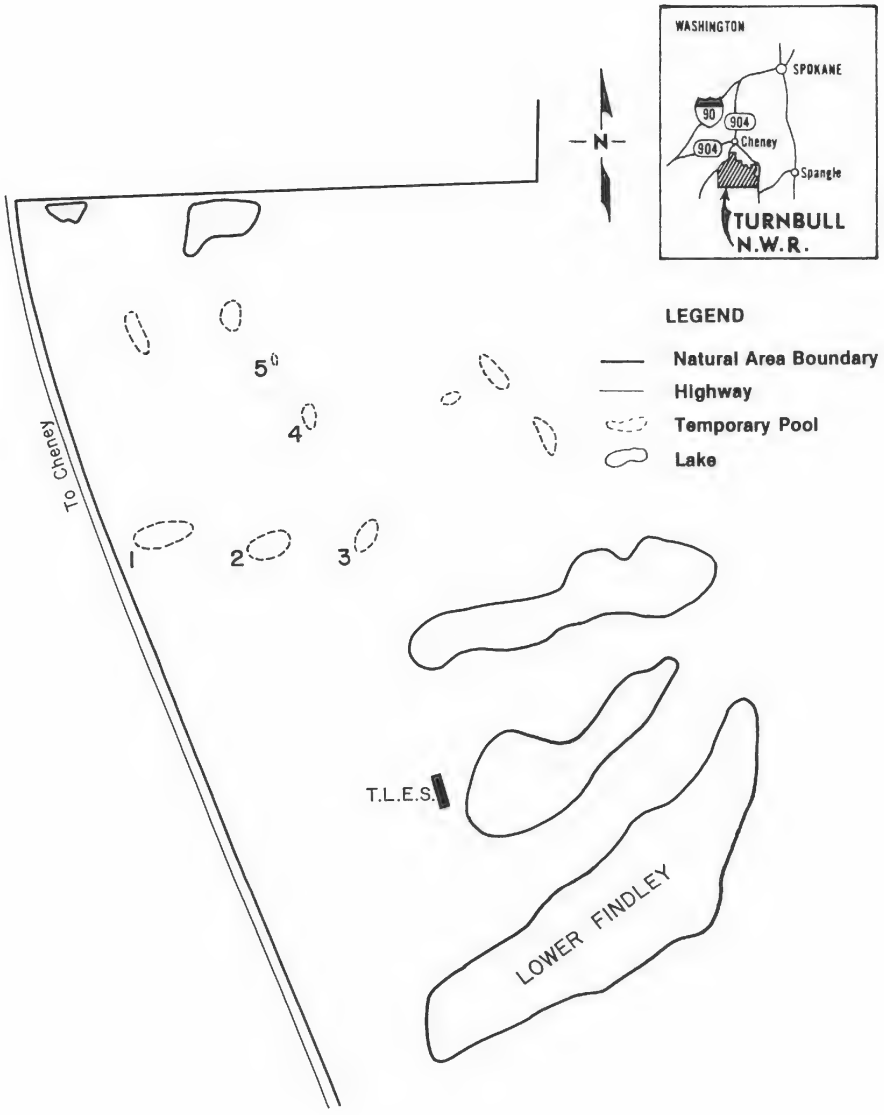

Figure 1. Location map of study area in eastern Washington. T.L.E.S. represents the Turnbull Laboratory for Ecological Studies.

aspen (*Populus tremuloides* Michaux) in their basins. The substrate is composed of needles of ponderosa pine and dead leaves and branches of aspen. In addition, some areas of most pools contain various grasses.

Methods

Sampling began on 20 February 1982, which was the first day water was found in the pools. Six days earlier, only snow existed in the basins and surrounding watershed. Rain and warming weather resulted in initial filling of pools. Sampling was continued each week until the pools dried up.

Six sampling stations were established in each of five pools during the fall of 1981. Two types of sampling stations were marked in each pool based on the presence or absence of dead limbs and branches of quaking aspen. Each type was paired together about 4 m apart to minimize differences caused by location within a pool. In addition, stations were selected so that depths would be uniform.

Quantitative samples of invertebrates were taken with a modification of the Wilding sampler (Wilding 1940). The sampler consists of a 1.25 m section of 10 cm plastic pipe with a closable aluminum valve on one end. The outer portion is made of two joints of 12.7 cm galvanized stovepipe. One side was marked in centimeters to facilitate measurement of the depth of each sample taken.

Samples were collected by quickly placing the stovepipe in the station area. The inner portion was then lowered into the stovepipe and the valve closed. The entire water column together with organisms inhabiting the surface of the bottom substrate was removed and filtered through a Wisconsin plankton net with 80 μm Nitex netting. It was assumed that all organisms isolated by the stovepipe were removed by the inner tube.

Invertebrates were separated from detritus by allowing the detritus to settle and then pouring the supernatant through a Wisconsin net. This process was repeated twice. The remaining detritus was placed in a coarse mesh net and washed into a Wisconsin net to remove any remaining invertebrates. This made it possible to count the taxa more easily. Samples were then preserved in formalin, stained with Eosin Y, and volumes were adjusted to 50 ml.

Density of organisms was estimated in the lab by taking two 5 ml subsamples with a Stenson-Hempel pipette (Edmondson 1971) and counting under a dissecting microscope at 24x magnification using a modification of the rotary counting chamber designed by Ward (1955).

The activity trap consists of a 4 l jar with a large funnel attached to the opening (Whitman 1974). Organisms swim into the traps and accumulate over a period of time. Two of these samplers were suspended in the water column in each of pools 1-3. After 24 hours, samples were removed, filtered through a Wisconsin net, and preserved in formalin.

Invertebrates were identified as to species when possible with the aid of Brooks (1957), Edmondson (1959), Pennak (1978), and Usinger (1963).

Results and Discussion

Approximately 30-45 cm of snow covered the study area prior to the first week in which water was observed in the pools. This condition persisted until 14 February at which time temperatures increased and precipitation began. Water accumulated in all pools by 20 February (Fig. 1). Maximum depth reached a peak on 6 March, decreased, and peaked again on 17 April. Depths decreased until pools 4 and 5 dried up shortly after 1 May (week 11). The last date that water was recorded in pool 1 was 5 June.

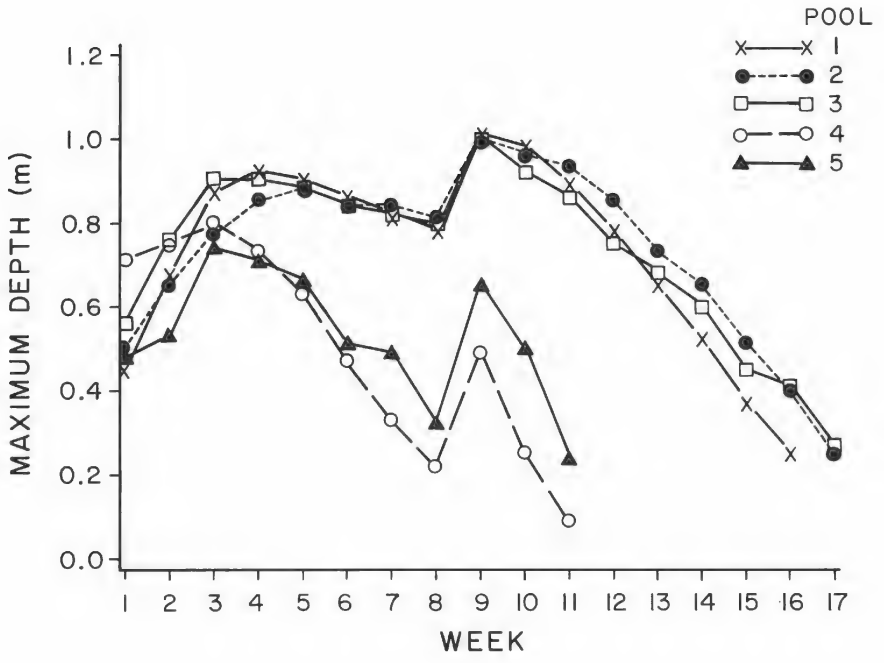

Figure 2. Weekly fluctuation in maximum depth.

The last date for pools 2 and 3 was 12 June. Small puddles of water existed in pools 2 and 3 as of 18 June. The maximum surface area ranged from approximately 250 m^2 for pool 5 to about 1400 m^2 for pools 1 and 2.

Maximum depth for pools 4 and 5, which was approximately 80 cm and 74 cm respectively, occurred during 6 March. Maximum depth for pools 1-3 was about 100 cm on 17 April.

Eight species of crustaceans were found in the pools (Table 1). These included four species of copepods (Copepoda), and one species each of seed shrimps (Ostracoda), water fleas (Cladocera), clam shrimps (Conchostraca), and fairy shrimps (Anostraca). Seven insects were also observed (Table 2). These represented two species of mosquitoes (Culicidae), four species of diving beetles (Dytiscidae), and one species of water strider (Gerridae). In addition, rotifers (Rotifera) and water mites (Acarina) were collected.

There were representatives of 17 taxa in pools 2 and 3, and 8 taxa in pool 5. With some exceptions, most species were found in all pools. Pool 5 did not contain the two

TABLE 1. Distribution of crustaceans found in five vernal pools.

Taxa	Pool 1	2	3	4	5
Class Branchiopoda					
Order Anostraca					
Eubranchipus serratus Forbes	X	X	X	X	X
Order Diplostraca					
Suborder Conchostraca					
Lynceus brachyurus Muller		X	X		
Suborder Cladocera					
Daphnia sp.*	X	X	X		
Class Ostracoda					
Order Podocopa					
Family Cypridae	X	X	X	X	X
Class Copepoda					
Order Calanoida					
Diaptomous novemdecimus Wilson	X	X	X	X	
Diaptomus hirsutus Wilson	X	X	X	X	
Order Cyclopoida					
Cyclops vernalis Fischer	X	X	X	X	X
Order Harpacticoida	X	X	X	X	X

*The **Daphnia** species present is either **D. pulex** Leydig or **D. middendorffiana** Fischer or a possible hybrid as discussed by Brook (1957).

TABLE 2. Distribution of insects found in five vernal pools.

Taxa	1	2	Pool 3	4	5
Class Insecta					
Order Hemiptera					
Family Gerridae					
Gerris buenoi Kirkaldy	X	X	X	X	
Order Coleoptera					
Family Dytiscidae					
Acilius semisulcatus LeConte	X	X	X	X	
Agabus sp. Leach	X	X	X	X	
Colymbetes sp. Clairville	X	X	X	X	
Rhantus sp. Dejean	X	X	X	X	
Order Diptera					
Family Culicidae					
Aedes cataphylla Dyar	X	X	X	X	X
Toxorhynchites sp. Theobald	X	X	X	X	X

Diaptomus species, and *Daphnia* species was only found in pools 1-3. *Lynceus brachyurus* was observed only in Pools 2 and 3.

Crustaceans observed in the vernal pools were compared with those collected in a permanent wetland approximately one km from the nearest pool (Table 3). Anostraca and Conchostraca were found in the pools but were not observed in the lake (Rabe and Gibson 1982). Cladocera and Calanoida occurred in both systems but were different species. Ostracoda and Cyclopoida had representative species in both habitats. Harpacticoids could not be distinguished because of taxonomic difficulties.

Free swimming insects that occurred in the pools consisted of Culicidae, Gerridae, and Dytiscidae (Table 2). No Culicidae were recognized in samples from Lower Findley Lake (Gibson, pers. comm.) and Gerridae were comprised of different genera from the two waters. Dytiscidae samples were not collected on a regular basis from the lake, so comparisons were not attempted.

TABLE 3. Comparison of number of species of crustaceans found in vernal pools and a permanent shallow lake.

Taxa	Pools	Lower Findley Lake
Anostraca	1	0
Conchostraca	1	0
Cladocera	1*	7
Ostracoda	1	1
Calanoida	2*	1
Cyclopoida	1	2
Harpacticoida	1	1

*Species different from those in lake.

In addition, 23 macroinvertebrates were collected in the lake (Rabe and Gibson 1982) but not the pools. Of these, species of *Hyallela, Gammarus, Chaoborus, Enallagma, Libellulidae,* Aeshnidae, *Hesperocorixa, Cenocorixa,* Hydrophilidae, Nepidae, *Callibaetis, Caenis,* Mesoveliidae, and Phryganeidae were observed during the period that the pools had water in them.

Apparently there is a significant difference in invertebrate community composition between temporary and permanent lentic systems. The lower number of taxa present in the vernal pools is probably caused by a lower diversity of microhabitats in the pools which are primarily lacking aquatic macrophytes. Secondly, organisms inhibiting vernal pools must cope with the dry phase or avoid it (Hartland-Rowe 1972). As one would expect, not all aquatic taxa are adapted to such an existence. Many species present in the vernal pools come under the classification of overwintering residents (Wiggins *et al.* 1980). These remain in the pool basin as encysted juveniles or as drought resistant eggs. All crustaceans and rotifers collected fit into this category.

As a result of seasonal variability in duration of vernal pools, organisms with r-selected characteristics are at an advantage over other organisms. Extending the number of generations in favorable years is also important. Taxa capable of parthenogenetic reproduction are suitable for these temporary environments (Wiggins *et al.* 1980). *Daphnia* species exhibited parthenogenesis until late in the season at which time drought resistant ephippia began to appear. Many other crustaceans are also capable of parthenogenesis (Pennak 1978).

The remaining taxa come under one of three additional classifications: overwintering spring recruits, overwintering summer recruits, and nonwintering spring migrants Taxa in these groups are capable of active dispersal (Wiggins *et al.* 1980).

Overwintering summer recruits, including mosquitoes of the genus *Aedes*, oviposit in the dry pool basin. Dytiscid beetles have been reported under both of the two remaining classifications, but Gerridae are classified as nonwintering spring migrants. Water mites fall into the same classifications as the dytiscid beetles (Wiggins *et al.* 1980).

The habit or mode of existence of invertebrates was determined by the use of activity traps and the modified Wilding sampler. The Wilding sampler collects forms from the water column and bottom surface whereas activity traps collect organisms only in the water column. Thus it was possible to compare the percentage occurrence in these two methods and subsequently classify all taxa according to their general habit.

Harpacticoids and nauplii are primarily benthic which is indicated by the higher percentage occurrence in the Wilding sampler (Table 4). In contrast, *Diaptomus* spp.,

TABLE 4. Weekly occurrence (expressed as a percentage of total samples for pools 1-3) of crustaceans collected by two sampling methods. A = Activity trap . W = Wilding sampler.

Week	Species															
	Diaptomus		**Cyclops**		Ostracods		**Eubranchipus**		**Daphnia**		**Lynceus**		Harpacticoids		**Nauplii**	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
1	—	0	—	100	—	100	—	58	—	42	—	0	—	92	—	100
2	0	0	88	100	100	100	38	81	0	0	0	0	50	75	75	100
3	13	22	88	100	75	100	38	72	17	0	0	0	50	89	100	100
4	100	89	100	83	75	100	50	89	50	0	0	0	13	89	63	100
5	100	94	88	78	50	89	38	78	17	6	25	42	0	83	75	100
6	100	94	83	72	83	83	67	83	0	0	0	25	0	83	17	100
7	100	78	50	61	50	100	67	78	17	11	0	25	0	89	17	94
8	100	83	33	72	50	78	33	56	17	0	0	0	17	78	0	89
9	100	94	50	56	33	72	17	22	33	22	0	8	0	61	17	94
10	100	94	50	72	100	83	17	50	33	39	0	17	0	83	0	100
11	100	78	50	83	100	78	67	33	67	72	0	0	17	94	33	100
12	100	78	33	89	100	89	33	28	100	50	0	0	0	89	0	100
13	100	81	67	100	67	100	67	50	33	75	50	0	17	88	17	94
14	100	80	50	93	100	100	33	7	50	80	100	0	17	73	0	100
15	100	83	0	100	100	92	0	0	50	83	100	25	0	50	0	100

Cyclops vernalis, Eubranchipus serratus, Daphnia sp., and Ostracoda are mostly planktonic as a result of similar occurrences in both samplers. *Lynceus brachyurus* shows a higher percentage in the Wilding sampler early in the study indicating a benthic existence. However, later there was a higher percentage in the activity traps, thus indicating a planktonic existence.

Similar results for rotifers and water mites are presented in Table 5. Both organisms

TABLE 5. Weekly occurrence (expressed as a percentage of total samples for pools 1-3) of rotifers, water mites, and insects collected by two sampling methods. A = activity trap. W = Wilding sampler. L = larvae. Ad = adults.

Week	Rotifera	Acarina		Culicidae		Dytiscidae	
	W	A	W	A	W	A	
						L	Ad
1	8	—	50	—	0	—	—
2	100	13	88	13	19	0	0
3	67	13	56	50	33	0	25
4	78	0	67	75	39	0	13
5	67	0	44	63	22	0	63
6	67	0	39	83	17	0	83
7	72	0	61	67	22	0	67
8	39	0	28	100	28	0	33
9	61	17	56	33	6	0	33
10	78	17	67	100	6	0	67
11	72	0	50	83	0	0	100
12	67	17	44	100	11	67	83
13	56	17	50	100	6	67	100
14	33	0	27	67	0	67	83
15	25	17	8	83	17	50	67

demonstrated a benthic existence since rotifers were not collected in the activity traps and water mites had a higher occurrence in the Wilding sampler.

All insects exhibited avoidance behavior (Table 5). Mosquitoes occurred in higher percentage in the activity traps, but the diving beetles were collected in activity traps only. Water striders were only collected with dip nets. Our data appears to support what has been reported in the literature regarding the habit of these invertebrates (Edmondson 1959, Pennak 1978).

Barlocher *et al.* (1978) observed that the dry phase of temporary pools results in higher protein levels in the detritus than would occur in permanent lentic systems. This may account for the large number of detritivores and filter feeders as shown in Figure 3. Taxa under this category include rotifers, harpacticoids, and nauplii which are primarily benthic as well as *Aedes cataphylla*, ostracods, and the branchiopods *Eubranchipus serratus, Daphnia* sp., and *Lynceus brachyurus*, all of which are mostly planktonic (Edmondson 1959, Pennak 1978). Some primary production was evident in the pools because of the observation of filamentous algae in the gut of *Diaptomus novemdecimus.*

A large number of predators were also present in this community (Fig. 3). The insects had the largest number of representatives. The planktonic *Toxorhynchites* species is known to feed on other mosquitoe larvae. *Gerris buenoi* is a surface dwelling predator and scavenger, whereas the Dytiscidae are swimming and diving forms (Merritt and Cummins 1978). Adult dytiscids were observed to prey upon adult *Eubranchipus serratus* in the lab and larvae have been reported to prey upon mosquitoe larvae (James 1969). Insects have the capability of actively leaving the system.

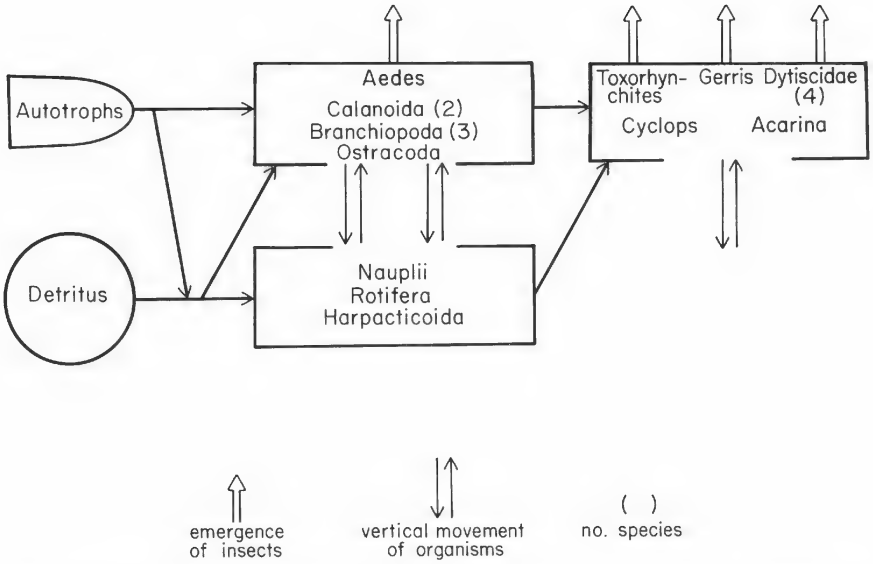

Figure 3. Mode of existence and trophic model for free-swimming invertebrates in vernal pools of eastern Washington.

Water mite larvae are parasitic upon insects such as the Culicidae, Gerridae, and Dytiscidae (Pennak 1978). However, nymphs and adults are predators which have been reported to prey upon ostracods (Wiggins *et al.* 1980). *Cyclops vernalis* is considered to be a predator among the species of crustaceans (Pennak 1978).

Acknowledgements

We thank Russell C. Biggam and Dr. Mark Knowden of the Department of Plant, Soil, and Entomological Sciences, University of Idaho for identification of the insects, and the Department of Biology at Eastern Washrington University for space provided at Turnbull Laboratory for Ecological Studies.

Literature Cited

Barlocher, F. R. J. Mackay, and G. B. Wiggins. 1978. Detritus processing in a temporary vernal pool in southern Ontario. Archives fuer Hydrobiology 81:269-295.

Bretz, J. H. 1923. The channeled scablands of the Columbia Plateau. The Journal of Geology 31: 617-649.

Brooks, J. H. 1957. The Systematics of North American Daphnia. Memoirs of the Connecticut Academy of Arts and Sciences, Volume XIII.

Daubenmire, R., and J. B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Washington Agricultural Experiment Station Technical Bulletin 60. Washington State University.

Donald, D. B. 1971. The Limnology of the Plankton of Three Temporary Ponds in Alberta. University of Calgary. M.S. Thesis.

Edmondson, W. T., editor. 1959. Freshwater Biology. Second Edition. John Wiley and Sons. New York.

———, and G. G. Winberg. 1971. A Manual on Methods for the Assessment of Secondary Productivity in Freshwaters. IBP Handbook No. 17. Blackwell Scientific Publications. Oxford.

Franklin, J. F., F. C. Hall, C. T. Dyrness, and C. Maser. 1972. Federal Research Natural Areas in Oregon and Washington, A Guidebook for Scientists and Educators. Pacific Northwest Forest and Range Experiment Station. U.S. Forest Service. Portland, Oregon.

Hartland-Rowe, R. 1966. The fauna and ecology of temporary pools in western Canada. International Association of Theoretical and Applied Limnology. Verhandlungen. Stuttgart. 16: 577-584.
———. 1972. The limnology of temporary waters and the ecology of Euphyllopoda. Pp. 15-31 in Clark, R. B., and R. Wooton, eds., Essays in Hydrobiology. University of Exeter.
James, H. G. 1969. Immature stages of five diving beetles (Coleoptera: Dytiscidae), notes on their habits and life history and a key to aquatic beetles of vernal woodland pools in southern Ontario. Proceedings of the Entomological Society of Ontario 100:52-97.
Kenk, R. 1949. The animal life of temporary and permanent ponds in southern Michigan. Miscellaneous Publication No. 71. Museum of Zoology, University of Michigan.
Merritt, R. W., and K. W. Cummins, editors. 1978. On Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa.
Pennak, R. W. 1978. Freshwater Invertebrates of the United States. Second Edition. John Wiley and Sons, New York.
Rabe, F. W., and F. Gibson. 1984. The effect of macrophyte removal on the distribution of selected invertebrates in a littoral environment. Journal of Freshwater Ecology 2(4):359-371.
Simpson, R. L., Jr. 1967. An Analysis of the Seasonal Succession of a Temporary Rainwater Pond in the central San Joaquin Valley, California. Fresno State College. M.S. Thesis.
Stout, V. M. 1964. Studies on temporary ponds in Canterbury, New Zealand. International Association of Theoretical and Applied Limnology. Verhandlungen. Stuttgart 15:209-214.
Usinger, R. L. 1963. Aquatic Insects of California. University of California Press, Berkeley.
Ward, J. 1955. A description of a new zooplankton counter. Quarterly Journal of Microscopical Science 96:371-373.
Whitman, W. R. 1974. The Response of Macroinvertebrates to Experimental Marsh Management. University of Maine. Ph.D. Thesis.
Whittaker, R. H., and C. W. Fairbanks. 1958. A study of plankton copepod communities in the Columbia Basin, southeastern Washington. Ecology 39:46-65.
Wiggins, G. B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. Royal Ontario Museum Publications in Life Scences 88:1-28.
———, R. J. Mackay, and I. M. Smth. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archives fuer Hydrobiologie Supplement 58:97-206.
Wilding, J. L. 1940. A new square-foot aquatic sampler. Limnological Society of America Special Publication No. 4.

Received December 20, 1982
Accepted for publication August 16, 1983

John W. Weber

Kwong-Chi Wu

Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164

and

Abholhassan Vafai

Shiraz University
Shiraz, Iran

Ultimate Loads for Shallow Funicular Concrete Shells

Abstract

Ten shallow funicular concrete shells (square base, double curvature, and different rises) were loaded to failure with a concentrated central force. Five shells were randomly reinforced with steel wires and the remainder with a wire mesh through the middle surface. All of the shells were 90 x 90 cm in plan form. Strain gages showed a linear relationship between load and strain in the elastic range of the concrete, whereas measured deflections varied nonlinearly with load. In addition, actual deflections were larger than those determined analytically by small deflection theory. These results indicate that large deflection theory, rather than classical small deflection theory, would be more appropriate for theoretical investigations of shallow funicular shells subjected to large concentrated loads. Ultimate loads were not clearly related to type of reinforcement, but were a function of the rise and thickness of the shell; in general, the larger the rise parameter (square of the ratio of rise to thickness), the larger the ultimate load. Failure patterns for shells with both kinds of reinforcement were the same.

Introduction

Because of their light weight, graceful form, and high load resisting capacity, shells of various types are used for many structural purposes. Although shells with potential use in construction have been studied by numerous investigators (Ramaswamy and Chetty 1959, Haas 1961, Ramaswamy 1968, Odello and Allgood 1970, Vafai and Farshad 1976, Farshad 1977, and others), there is a paucity of information on the ultimate strength of funicular shells with different rises. In the case of shells with double curvature (the type discussed herein), classical methods of analysis are complex and unwieldy. The development of the finite element method renders the analysis of such problems tractable, but experimentation is still needed to determine the actual behavior of shells with different reinforcement under various loading conditions; ultimate load and mode of failure are best determined experimentally.

Concrete Mix and Properties

Composition of the concrete mix is shown in Table 1.

Young's modulus, E, was determined by compressive test of standard cylindrical specimens (15.2 x 30.5 cm) cured under the same conditions as the shells. Values of E and other properties of the shells are given in Table 2. A value of 0.10 was used for Poisson's ratio.

TABLE 1. Concrete mix proportions for 1.0 m^3.

Mix Component	Amount
Portland cement	1790. kg
Coarse aggregate—traction sand	2130. kg
Fine sand	3690. kg
Water	235. liter
Air entrainment	0.036 kg
*Steel wires (25.4 x 2 mm)	224. kg

*For five randomly reinforced shells; the other five were reinforced with wire mesh (ordinary chicken wire) through the middle surface.

TABLE 2. Properties and failure loads, P_u, of shells.

Shell no.	Reinforcement	Rise, z (cm)	Thickness, d (cm)	$\lambda = \frac{z^2}{d}$	E(x 106) (N/cm2)	P_u (N)	$P_u b^2/Ed^4$
1	RR1	5.61	1.80	9.71	1.655	6,580.	0.835**
2	RR*	5.99	3.00	3.99	1.655	—	—
3	RR	6.30	2.50	6.35	1.379	12,230.	0.502
4	RR	7.01	2.20	10.15	.965	14,230.	1.391
5	RR	7.80	3.80	4.21	1.103	13,340.	0.128
6	WM2	6.91	2.20	9.86	1.517	16,680.	1.038
7	WM	7.39	3.30	5.01	1.517	21,130.	0.259
8	WM	7.80	2.80	7.76	1.517	20,240.	0.480
9	WM*	8.99	2.79	10.36	1.517	—	—
10	WM	9.80	3.30	8.82	1.517	37,360.	0.458

1Random reinforcement (mild steel wires, 2.54 x 0.20 cm).

2Wire mesh (ordinary chicken wire) through middle surface.

*Ultimate loads unrecorded.

**$P_u b2/Ed4$ computed with b = 47.0 cm for all shells.

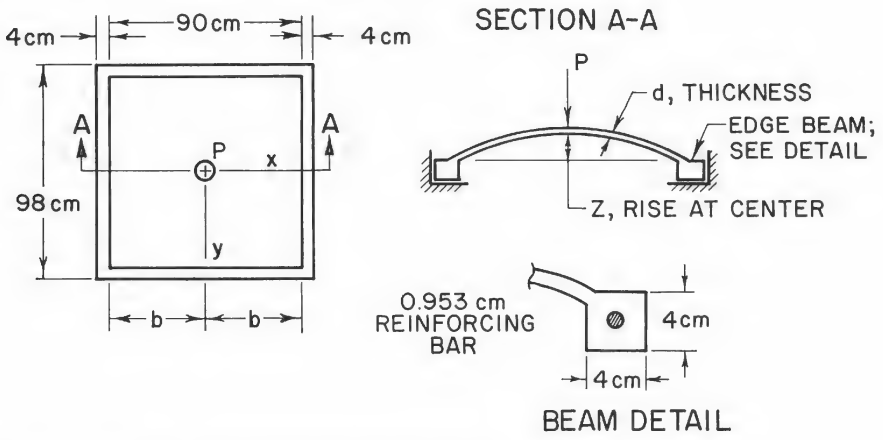

Figure 1. Funicular shell: dimensions, loading, and coordinate system.

Casting of Shells

A form consisting of a square steel frame and canvas was used for casting the shells. The canvas was stretched between the boundaries of the frame and clamped thereto.

When concrete was poured, the resultant sag (and therefore the rise of the shell when in inverted position) was determined by the tension in the canvas; thus, a funiculus was formed. Construction of the frame allowed the casting of four edge beams as integral components of each shell. All shells were moist-cured for 28 days before testing.

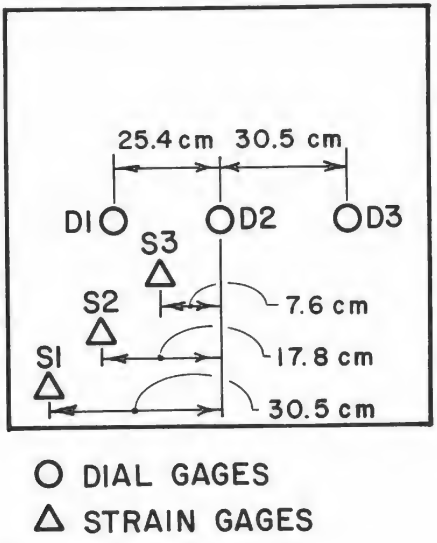

Figure 2. Location of gages (D2 at shell's center).

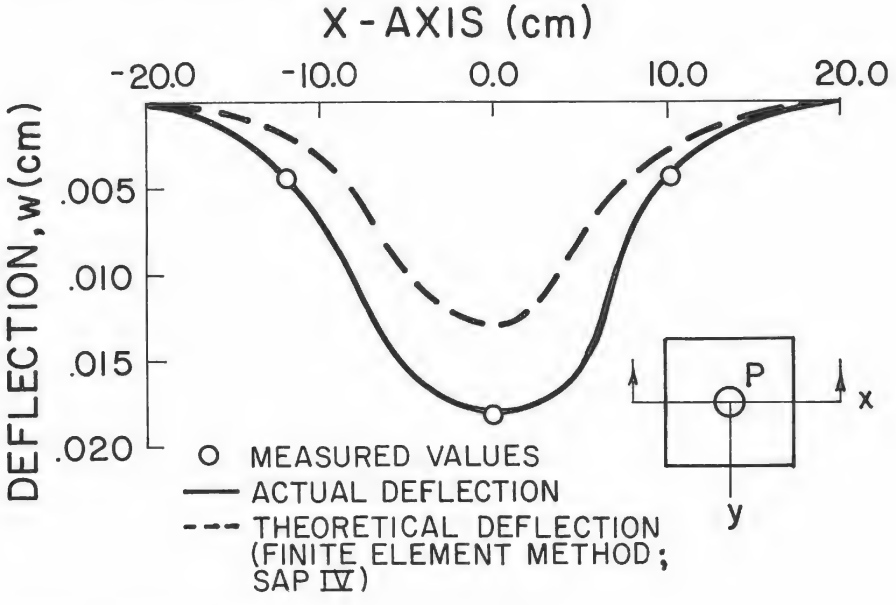

Figure 3. Typical deflection curve (shell no. 4, P = 2020 N).

Instrumentation and Testing

Electrical resistance strain gages (60° strain rosettes) were mounted on the upper and lower surfaces of each shell at intervals along a diagonal, and dial gages were installed to record deflections at several locations along a transverse section through the middle of the shells (Fig. 2). Each shell was loaded in the elastic range, and strains and deflections recorded. After non-destructive testing, all shells were loaded to failure.

Results and Discussion

Measured deflections, as shown in Fig. 3 for a typical case, are large in the region of

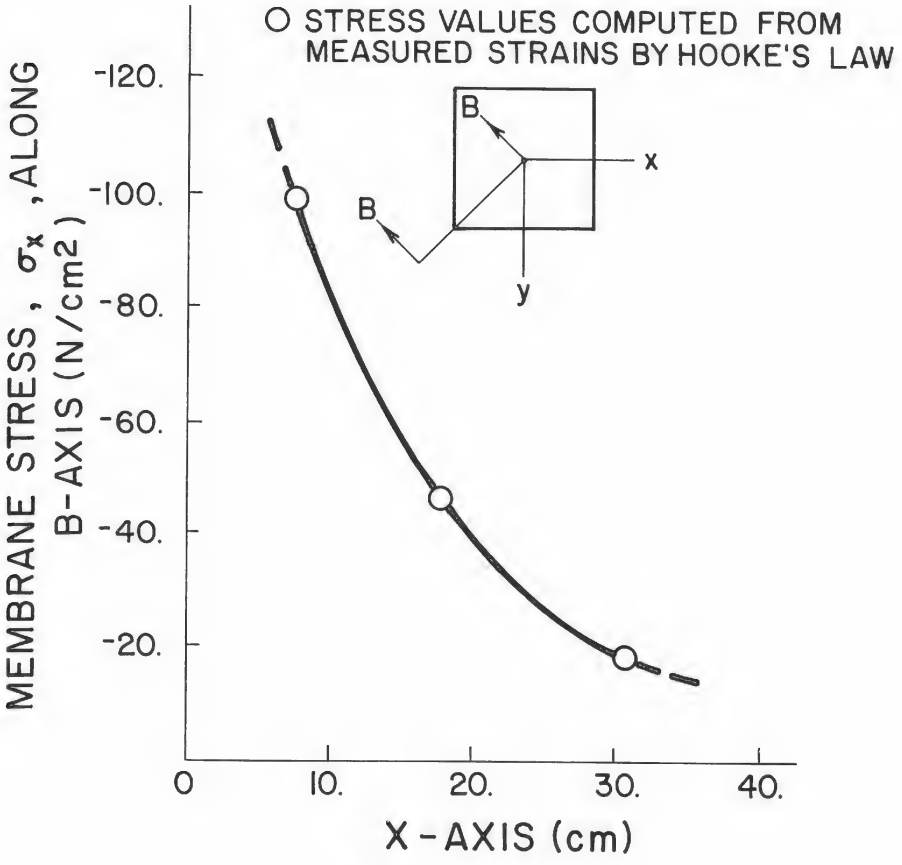

Figure 4. Typical elastic membrane stress curve along B-axis (shell no. 2, P = 4450 N).

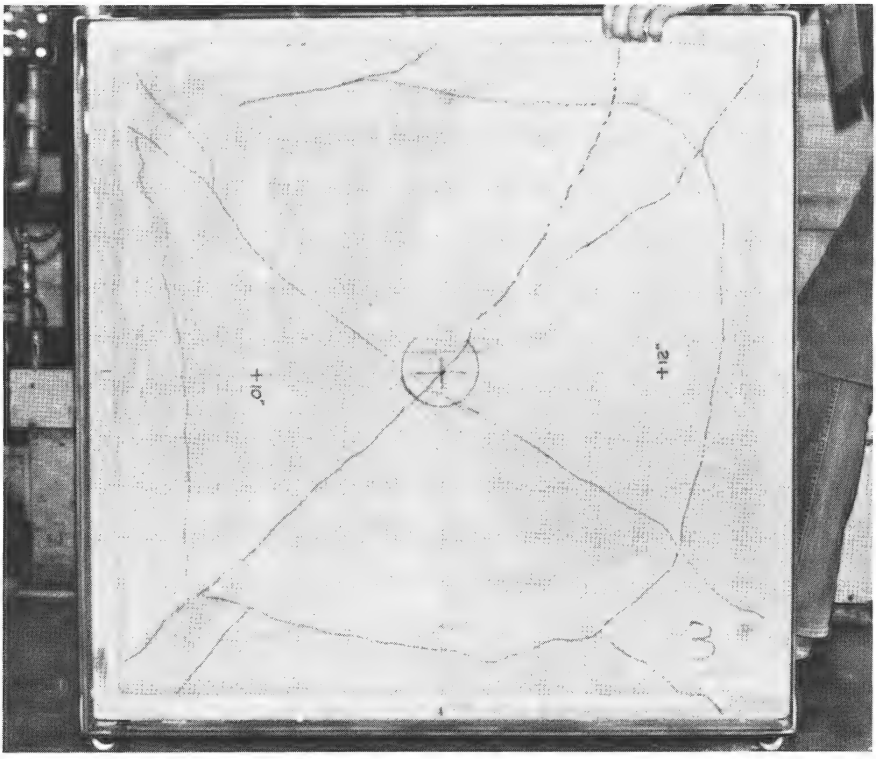

Figure 5. Crack patterns for a typical case (shell no. 3).

the centrally applied force and comparatively small elsewhere. Fig. 3 also shows that measured deflections are greater than those determined analytically by the finite element method (Sap IV thin shell element program with 16 rectangular elements for one quadrant of the shell).

Assuming that bending is localized in the vicinity of the supports and point of load application, membrane theory can be used to approximate the behavior of the shells investigated. A plot (Fig. 4) of the membrane stress distribution (as determined by Hooke's Law from measured strains) for a typical case shows a steep gradient in the vicinity of the load.

At large deflections just before failure, shells with both kinds of reinforcement exhibited the same sequence of crack propagation and crack pattern. Visible cracks first appeared at the center of a shell's outer surface and then propagated to the corners along the diagonals. As the load was increased, apparent zones of tension near and approximately parallel to the supports also cracked (see Fig. 5), forming a mechanism by which the shell eventually failed. Zones of tension in the vicinity of the supports can be attributed to localized bending caused by support reactions.

Although strain measurements indicate a linear variation of strain with load in the elastic range, dimensionless load-deflection plots (Fig. 6) illustrate that load and deflection vary nonlinearly. This behavior and the discrepancy between measured and

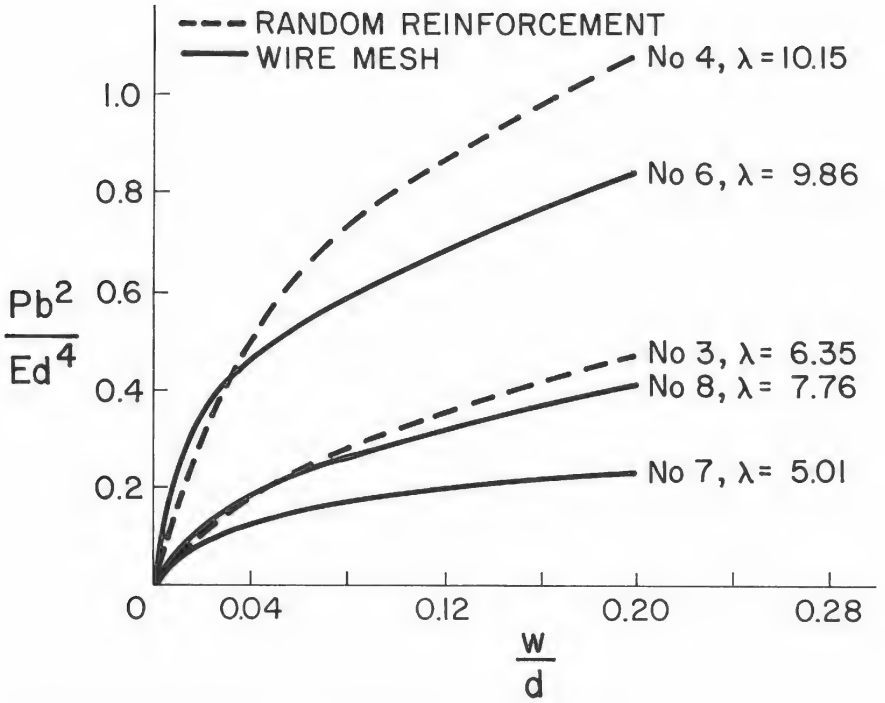

Figure 6. Dimensionless load-center deflection curves for several cases.

theoretical deflections (Fig. 3) suggest that mathematical investigations of shallow funicular shells with large concentrated loads should be based on large deflection theory. Fig. 6 also indicates that the deflection characteristics of a shell vary closely with its rise parameter, λ; type of reinforcement (for the shells tested) appears to have little effect on deflection.

The dimensionless plot in Fig. 7 shows the variation of the failure load, P_u, with λ. In general, P_u increases with large values of λ. For the shells tested, Fig. 7 shows that the load resisting capacity of a shell, regardless of the kind of reinforcement, is primarily a function of its rise and thickness. By Fig. 7, the relationship between P_u and λ can be approximated by the equation ($2 \leqq \lambda \leqq 11$)

$$\frac{P_u b^2}{Ed^4} = 0.0603e^{0.2197\lambda}$$

Extrapolation of the dimensionless results in Fig. 7 to shallow funicular shells different in size from those discussed in this study requires caution, since other modes of failure are possible. For example, Odello and Allgood (1970), who tested funicular shells 10.67 x 12.20 m in plan with a 5.08 cm thickness and a 76.2 cm rise ($\lambda = 225$), found that uniformly loaded shells failed by buckling and that shells subjected to concentrated loads failed by punch shear. Additional experimental work on shells of sizes transitional between those discussed herein and those considered by Odello and All-

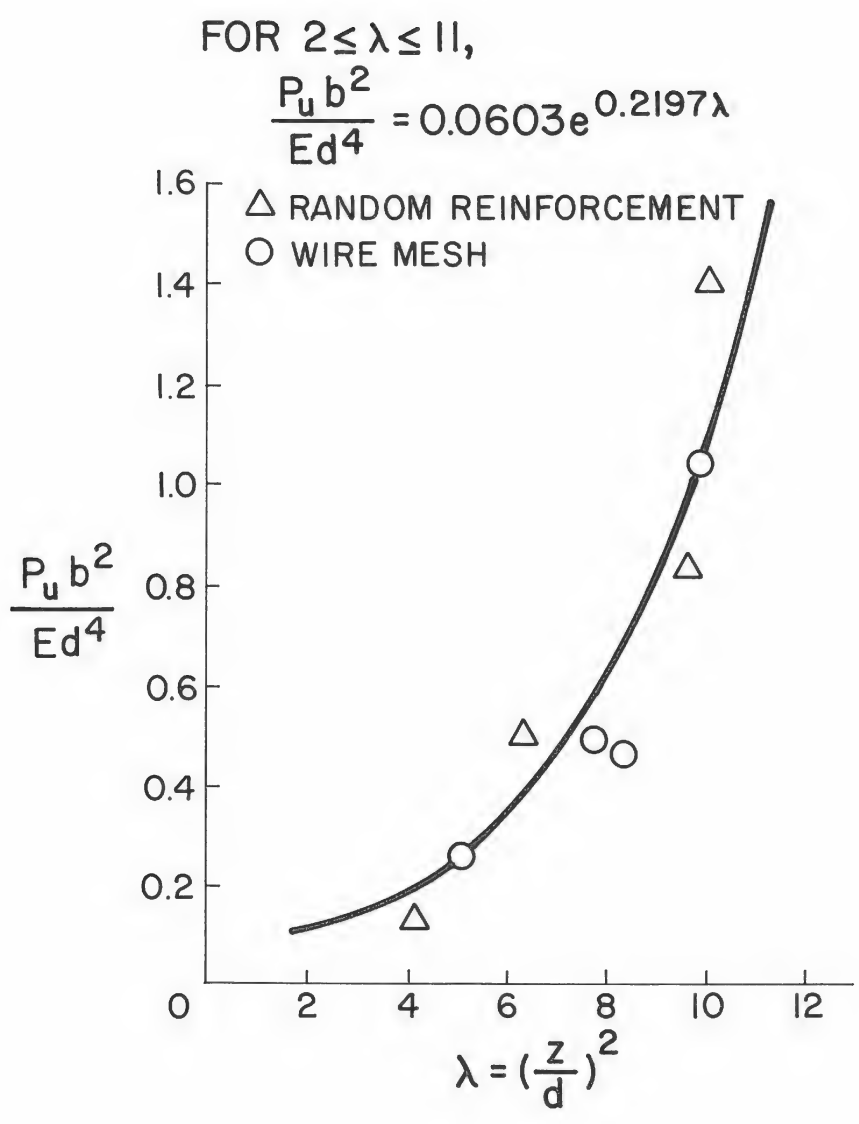

Figure 7. Variation of ultimate load parameter, $P_u b^2/Ed^4$, with rise parameter, λ.

good should be undertaken to further the understanding of failure loads for funicular shells.

Acknowledgments

The writers thank R. J. Hoyle, Washington State University, for his laboratory assistance.

Literature Cited

Farshad, M. 1976. Shell Structures. Shiraz University Press, No. 84. Shiraz, Iran.
Haas, A. M., and A. L. Bouma. 1961. Shell research. Proceedings of the Symposium on Shell Research, Delft. North Holland Publishing Co., Amsterdam.
Odello, R. J., and M. R. Allgood. 1970. Concrete funicular shells for floors and roofs. Technical Report R-693, YF 38.534.001.01.003. Naval Civil Engineering Laboratory, Port Hueneme, Calif.
Ramaswamy, G. S. 1968. Design and Construction of Concrete Shell Roofs. McGraw-Hill, N.Y.
———, and S. M. K. Chetty. 1959. A new form of double-curved shell for roofs and floors. The International Association for Shell Structures. Bulletin 1. a-4. Internation Colloquium on Construction Processes of Shell Structures, Madrid, Spain.
Vafai, A., and M. Farshad. 1976. Investigation of pointed domes—II. Experiment. Building and Environment 11:87-90.

Received December 26, 1982
Accepted for publication April 19, 1983

Matthew H. Dick

Department of Biology
Western Washington University
Bellingham, Washington 98225

Bryozoan Behavior in Relation to Autocleaning in Holoporella brunnea (Hincks)

Abstract

The marine bryozoan *Holoporella brunnea* exhibits autocleaning behavior. Its zooids use well-developed, abfrontally-placed tentacular spines to scrape the colony surface. Autocleaning is homologous with, and has evolved from, ejection behavior, which is common among marine bryozoans. Hypothetical steps in the evolution of autocleaning included increased zooid size, tentacle elongation, colony integration, and the pronounced development of preadapted tentacular spines, the original function of which may have been to remove debris from around the zooidal orifice. None of these characteristics are exhibited by the living species *Hippothoa hyalina* which may display the relatively simple behavior of the small ancestral bryozoan. Intermediate stages of the evolution of autocleaning are seen in the living bryozoans *Eurystomella bilabiata* and *Rhynchozoon* sp., as well as in *H. brunnea* itself. Ejection behavior involves a complex of reflexes in which there are several levels of response to different levels of stimulus. Autocleaning and writhing behavior form a similar reflex complex. Bryozoan behavior is characterized by chain reflexes both within and between these behavioral complexes and is more complicated than previously suspected.

Only recently have bryozoologists begun to determine the full range of behavior performed by bryozoan autozooids, the feeding individuals that comprise the bulk of a bryozoan colony. Winston (1978, 1979) described and categorized autozooid behavior and colony function in numerous tropical Atlantic and temperate Pacific coast bryozoans. While making extensive behavioral observations on various bryozoan species, including some of those treated by Winston (1979), I became aware of the fact that bryozoan behavior is much more complex than previously believed, and that it could be analyzed with a comparative approach similar to that commonly applied to vertebrates and some higher invertebrates.

The purpose of this paper is twofold. First it shows the relationship of lophophoral flattening to autocleaning in *Holoporella brunnea* (Hincks) (Phylum Bryozoa, Order Cheilostomata, Suborder Ascophora), and presents a hypothesis on the evolution of autocleaning from ejection behavior, a trait widespread among bryozoans. Second, using autocleaning and ejection behavior as examples, it demonstrates that bryozoan behavior consists of complexes of traits, each trait a reflex response separated from other traits by stimulus thresholds. Behavioral complexes are likewise separated from other complexes by thresholds.

Some structural and behavioral traits will be described in three ascophoran bryozoans other than *Holoporella brunnea*, insofar as these species represent possible intermediate stages in the evolution of autocleaning. *Hippothoa hyalina* (Hincks) of the Hippothoidae, a family generally assumed to be primitive among the Ascophora (Ryland 1970), is here considered to be similar to the ancestral form, and *Eurystomella bilabiata* (Hincks) and *Rhynchozoon* sp. are considered to represent more advanced

forms. In each of these species, ejection behavior, zooid size, degree of colony integration and tentacle morphology are described.

Methods

Bryozoans were observed at the Hopkins Marine Station, Pacific Grove, California, between 13 February and 18 March 1973. *Holoporella brunnea* was readily obtained from floats in the Monterey Boat Harbor. Other species were obtained intertidally at Pacific Grove and Point Pinos. The bryozoans were kept in running-seawater aquaria and either placed in culture dishes for short periods of observation or observed directly through the sides of the aquaria with a stereomicroscope. For measurement, illustration, and the study of tentacle structure, whole colonies and slide preparations of removed polypides were photographed through a compound microscope. The system of Winston (1978), in which there are seven types of colony behavior, is used throughout this paper in describing degree of colony integration (see Key to Table 1).

Results

Autocleaning Behavior

Holoporella brunnea (Fig. 1) forms well integrated, Type 5 colonies in which polypides

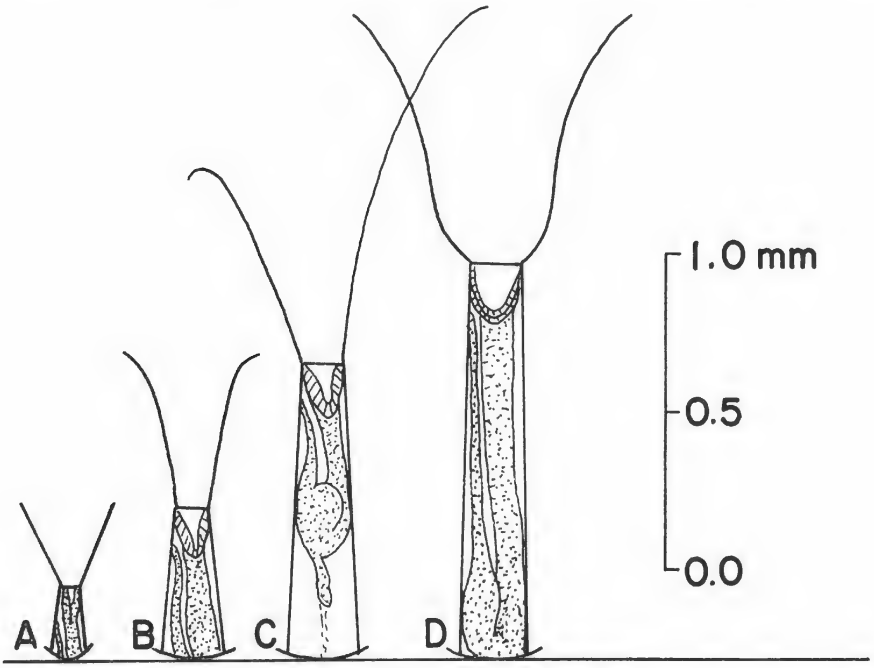

Figure 1. Comparative size of zooids: A, *Hippothoa hyalina*; B, *Holoporella brunnea*, equitentacled form; C, *Holoporella brunnea*, obliquely ttruncate form; D, *Eurystomella bilabiata.*

form fixed clusters, and the clusters are enhanced by an irregular patterning of the colonial skeleton. Lophophores have two forms: the equitentacled type (Fig. 1B) in incurrent zones and the obliquely truncate type (Fig. 1C) around excurrent zones.

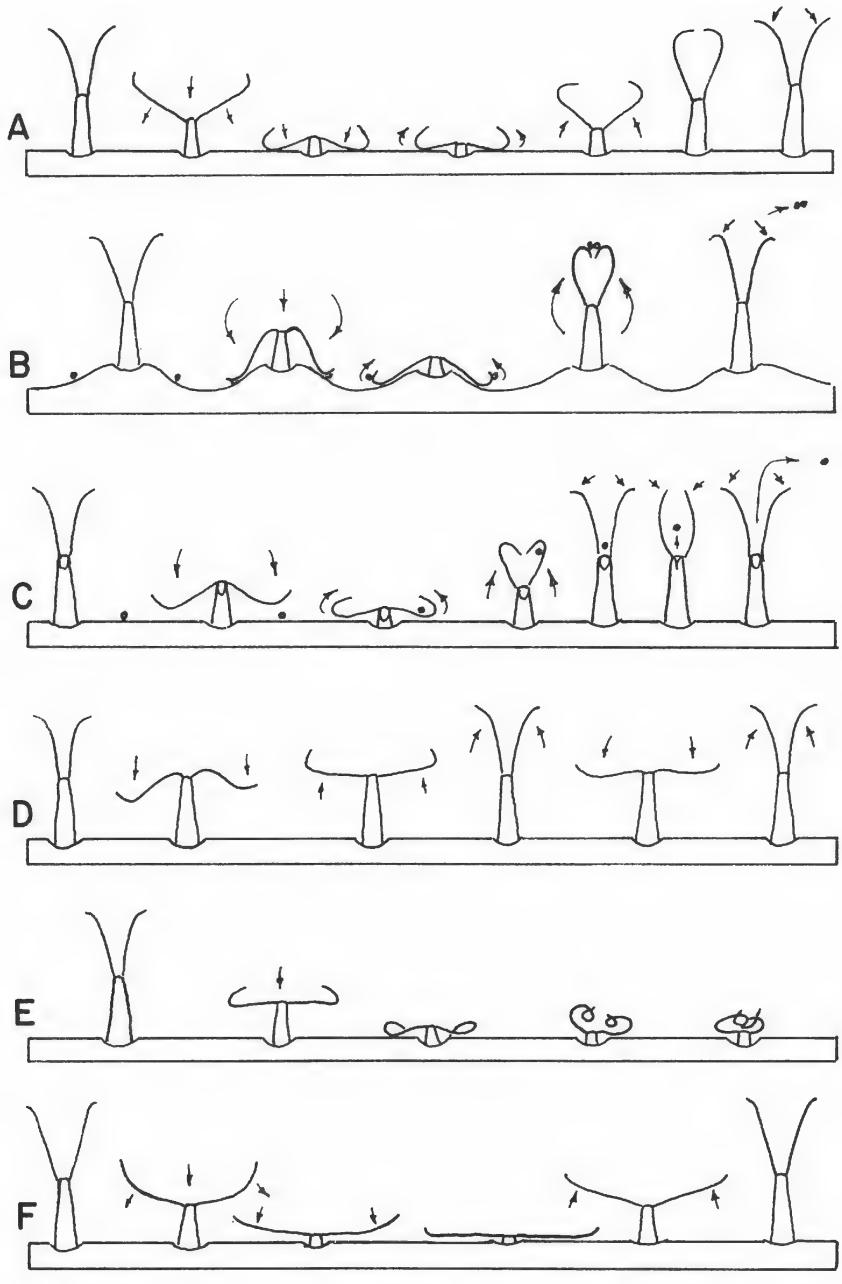

Figure 2. Autocleaning and related behavior: A-E, *Holoporella brunnea* A, basic autocleaning motion; B, particle collection and elimination; C, scooping of particle inside lophophore; D, incomplete autocleaning; E, writhing. F, *Rhynchozoon* sp., rudimentary autocleaning.

Every autopolypide of *H. brunnea* is capable of what is here termed autocleaning behavior (Figs. 2A-C), in which the polypide partially retracts and simultaneously swings its tentacles downward until the abfrontal surfaces of the tentacles touch the cystids. The polypide continues to retract as the tentacles slide along the colony surface away from the orifice.

On the distal three quarters of each tentacle are 11 to 17 bifurcate spines (Fig. 3), each about 30 μm long, situated abfrontally between two rows of red-pigmented lateroabfrontal cells. The proximal few spines are shorter and finer than the rest. Spines are enlarged at the base where they extend from the tentacle and are partially retractable. Spines are, to some extent, also moveable in the median plane of the tentacle. Although the spines usually point distally, I occasionally saw a few of them perpendicular to the tentacle or pointed proximally. The lateroabfrontal cells terminate in a clump of red-pigmented cells at the tentacle tip. The terminal clump appears to secrete an adhesive substance, because particles often stick to the tentacle tips (Fig. 3B).

Under low magnification (X15), I observed the tentacles sliding with a jerking motion during autocleaning, indicating that the spines were moving across the colony surface. Under higher magnification (X60), I observed the spines actually scraping the cystids and catching, now and then, on surface irregularities, thus producing the jerking motion. The portion of the tentacles that takes part in autocleaning varies. Often the distal ends of the tentacles are curved away from the colony surface as the polypide retracts, thereby erecting the spines (Fig. 3A). Usually the spineless, proximal one-quarter of a tentacle does not touch the cystid. During autocleaning, polypides brush not only their own cystids, but also adjacent cystids and the tentacle sheaths of adjacent polypides.

Particles on the colony surface are either loosened by the spines and swept away by the excurrent flow of the colony, or they are picked up by the spines and carried upward. If the latter occurs, the tentacles remain bent and converge at the lophophore axis, and their tips point toward the mouth (Fig. 2B). The lophophore then unfolds, flinging away the consolidated particles which are perhaps held together by secretions from the cells at the tentacle tip. Occasionally particles between two tentacles are scooped up by the tentacles and carried into the lophophore; these are eliminated by either rejection or ejection behavior (Fig. 2C). Polypides commonly perform incomplete cleaning motions. They retract slightly or not at all, swinging the tentacles toward the colony surface without touching it (Fig. 2D).

Polypides autoclean during the normal feeding activity of a colony, often as a result of no apparent stimulus. Obliquely truncate polypides autoclean more frequently than equitentacled polypides. Autocleaning increases sharply in frequency when a heavy load of particulate matter is dropped onto a colony. Touching a polypide anywhere with a probe elicits autocleaning. Heavy mechanical stimulation of a polypide causes writhing behavior, previously seen in *H. brunnea* by Winston (1979), in which the polypide retracts to orifice level and crosses and curls the tentacles over the lophophore base (Fig. 2E). Though writhing appears to be related to autocleaning, its function is unknown. Stimuli other than tactile ones can cause both autocleaning and writhing. When a bright microscope light is directed onto undisturbed feeding colonies in an aquarium with circulating seawater, there is a gradual but great increase in the frequency of autocleaning, then of writhing, within 5-10 minutes. Colonies removed from aquaria

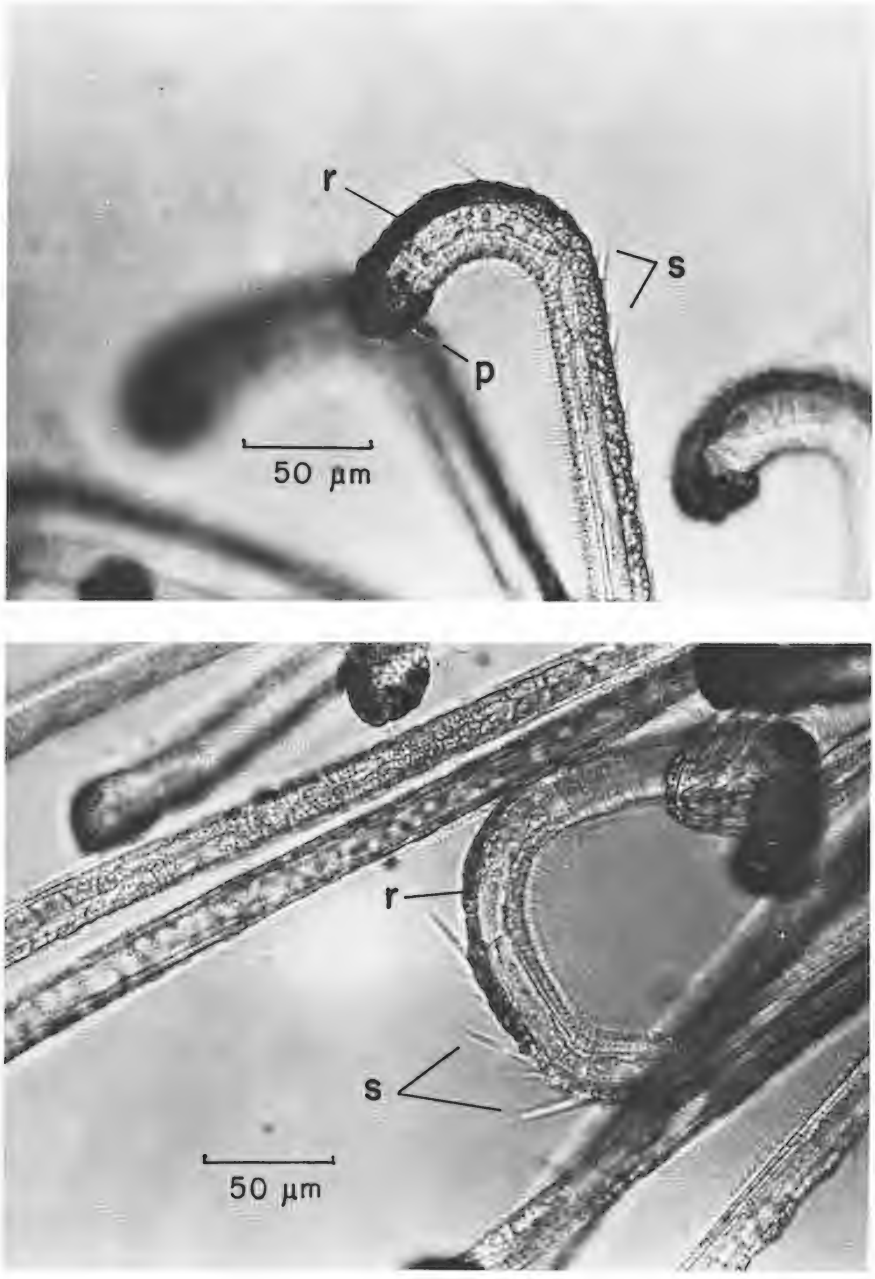

Figure 3. Abfrontal tentacular spines in *Holoporella brunnea*: A, erection of the spines (s) by tentacular curling, r = red-pigmented lateroabfrontal cells; B, tentacle tip with particle (p) adhering.

into finger bowls show an increase in the frequency of autocleaning and writhing with time, perhaps due to a decrease in dissolved oxygen or an increase in temperature.

Ejection Behavior

Previous authors have used the terms ejection and rejection interchangeably, or have used rejection to indicate any mechanism for eliminating unwanted particles from the lophophore (Winston 1978). Ejection and rejection are two quite distinct behavioral complexes and should not be confused with one another. In the present paper, ejection means the elimination of medium- to large-sized particles from the lophophore by one or more of the following processes: 1) pharyngeal contraction, 2) reversal or cessation of activity of the lateral tentacular cilia, 3) coordinated motions of all the tentacles, and 4) a flinging motion performed by the entire polypide. Rejection means the elimination of small- to medium-sized particles by one or more of the following processes: 1) action of the pronounced ciliary rejection tracts or ciliated groove ventral to the mouth, 2) the motions of the rejection tentacles, which are the most ventral two tentacles, sometimes coordinated with movement by one or both of the two feeding tentacles adjacent to them, and 3) the action of the frontal ciliary tracts on the rejection tentacles which carry particles distally and not proximally as on all other tentacles.

Zooids of *Hippothoa hyalina* (Fig. 1A) are considerably smaller than those of *Holoporella brunnea*, and form Type 3 colonies, with polypides functioning more at the individual level. During ejection the initial motion of the particle seems to result from pharyngeal contraction. Occasionally small particles are ejected by this means alone. For a larger particle, all the tentacles are flicked suddenly outward (Fig. 4A). This changes the current vectors so that the particle moves upward. Borg (1926) and Bullivant (1968) observed cessation and reversal of beat of the lateral tentacular cilia. Although I was unable to verify their observations, it would be difficult for ejection to occur without a change in the powerful feeding current. Whatever the specific mechanism, the tentacular motion is usually enough to eject the particle. After several unsuccessful attempts at this means of ejection, the polypide retracts quickly, though not completely, thereby moving out from under the particle (Fig. 4A). An extremely large particle is ejected by a strong downswing of all the tentacles followed by partial retraction (Fig. 5A). In this response, the same behavioral elements that occur in autocleaning are evident: tentacular downswing and partial polypide retraction.

Zooids of *Eurystomella bilabiata* (Fig. 1D) are larger than those of *H. brunnea* and much larger than those of *H. hyalina*, and they form Type 3 colonies. As in other species, the first step in ejection is the upward motion of the particle due to pharyngeal contraction and perhaps ciliary cessation or reversal. The tentacles all sweep gracefully inward toward the lophophore axis to expel the particle (Fig. 4B). If this is unsuccessful, the whole polypide then bends to one side, flinging the particle away as it performs the ejection motion (Fig. 6A). This type of behavior is here termed "flinging," and it is random in *E. bilabiata*, with the particle being ejected in no particular direction. If repeated ejection attempts fail, or if a very large particle falls into the lophophore, the polypide partly retracts, swinging all the tentacles toward the colony surface. The particle rolls off the lophophore base and down the frontal surfaces of several tentacles (Fig. 5B). As in *H. hyalina*, the same behavioral elements that occur in autocleaning—

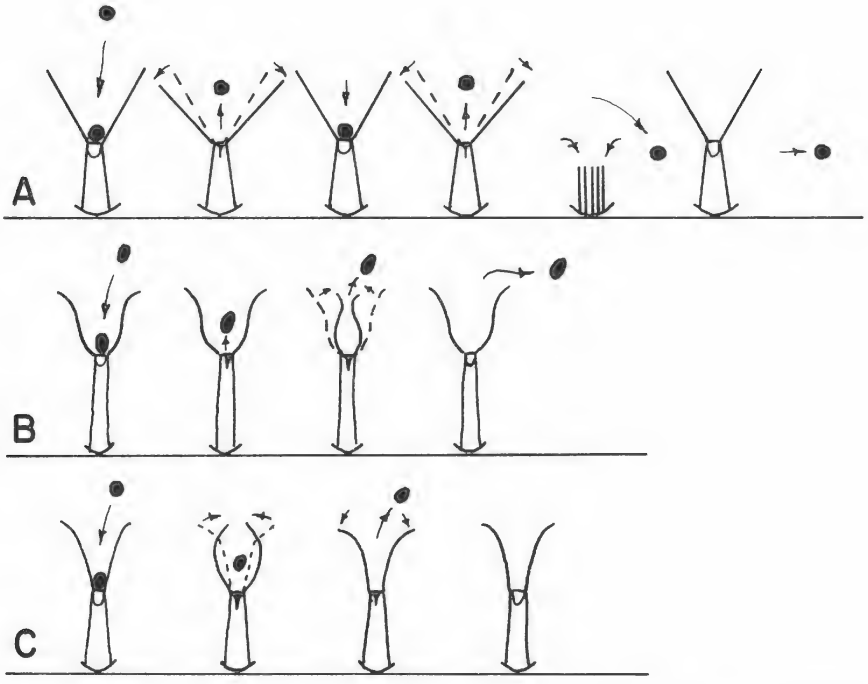

Figure 4. Simple ejection response: A, *Hippothoa hyalina*; B, *Eurystomella bilabiata*; C, *Holoporella brunnea.*

tentacular downswing and partial retraction—are present in the extreme ejection response.

Holoporella brunnea ejects medium-sized particles by first swinging the tentacle tips inward toward the lophophore axis as the pharynx contracts. The tentacles then snap back to the feeding position, and the water forced from the lophophore ejects the particle (Fig. 4C). Obliquely truncate lophophores eject medium- to large-sized particles by flinging (Fig. 6B), always in the direction of the longest tentacles, and consequently in the direction of excurrent flow. Polypides eject very large particles with a motion (Fig. 5C) simliar both to autocleaning and to the extreme ejection response of *E. bilabiata.* First, the pharynx contracts as the tentacle tips swing toward the lophophore axis. The polypide then quickly retracts, creating an opening in the tight lophophore sheet. The strong excurrent flow emerging from the opening carries away the particle. The extreme ejection response of *H. brunnea* is quite similar to, and often immediately followed by, the incomplete autocleaning motion (Fig. 2D).

Rhynchozoon sp. forms circular, Type 5 encrustations, and has both equitentacled and obliquely truncate polypides. It is thus at the same level of organization as *H. brunnea. Rhynchozoon* sp. performs a range of ejection motions similar to those just described in several species. In addition, it performs a rudimentary autocleaning motion in which polypides retract almost flush with the secondary orifice and lay the tentacles down flat onto the colony surface (Fig. 2F). *Rhynchozoon* sp. does not place the

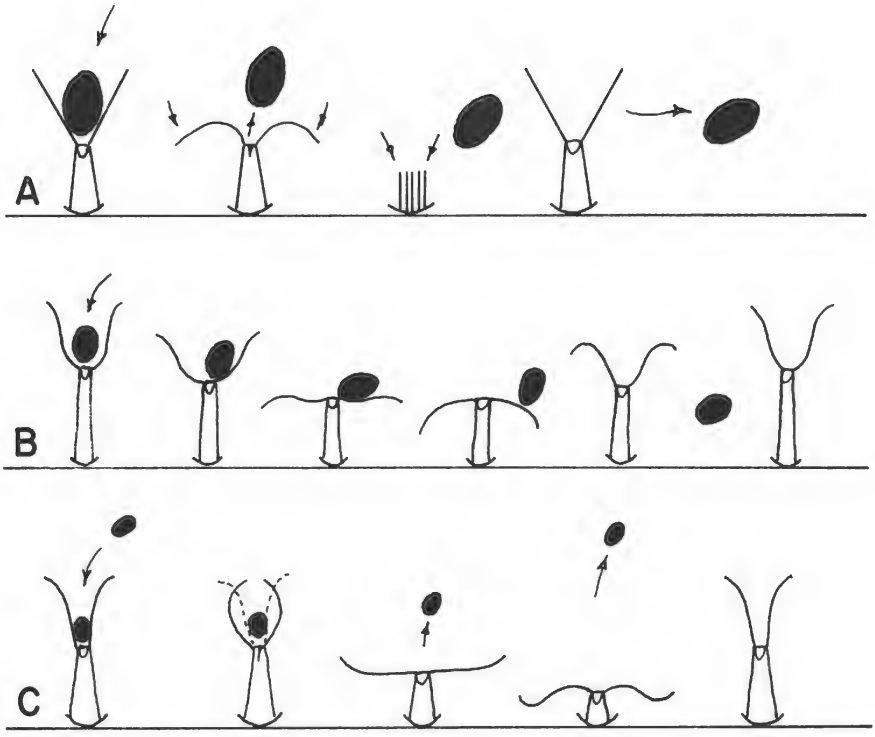

Figure 5. Extreme ejection response: A, *Hippothoa hyalina*; B, *Eurystomella bilabiata*; C, *Holoporella brunnea.*

tentacles onto the colony surface while continuing to retract, nor does it curl the tentacles distally to erect the spines, and therefore does not rasp the colony surface as does *H. Brunnea.* The rudimentary autocleaning motion of *Rhynchozoon* sp. is quite similar in form to the incomplete autocleaning motion of *H. brunnea*, except that, in the latter case, the polypide does not retract to orifice level.

Tentacle Morphology

Abfrontal structures. Recent authors, including Bullivant (1968), Gordon (1974) and Winston (1978), have described various bristlelike structures on the ends and abfrontal surfaces of tentacles. Their observations are important, because some of the structures they describe are probably homologous with the heavy spines utilized by *Holoporella brunnea* for autocleaning. Gordon (1974, Fig. 3) showed "tufts of cilia" which appear stiff alternating with long, flexible, solitary cilia. Winston (1978, Fig. 7) showed stiff-appearing "end tufts of cilia" and non-motile single cilia. A great deal of confusion exists in this terminology as to what constitutes a cilium, bristle, or spine. In this paper, the term cilium is reserved for a fine structure capable of flexible movement. A bristle is any stiff, more or less fine, non-motile structure. Very coarse bristles

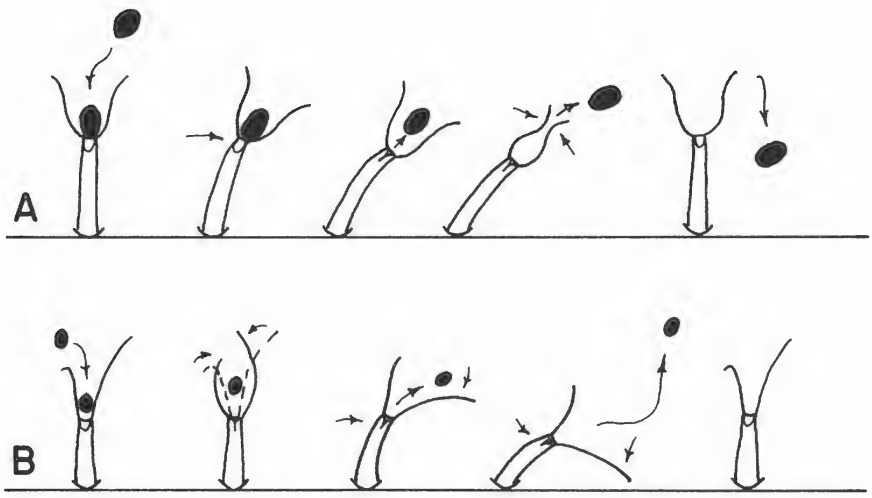

Figure 6. Ejection by flinging: A, *Eurystomella bilabiata*; B, *Holoporella brunnea.*

are here referred to as spines. To determine whether bristles and spines are homologous with cilia requires ultrastructural examination.

Hippothoa hyalina bears occasional fine bristles on the abfrontal surface and tip of each tentacle. In *Eurystomella bilabiata*, the proximal portion of each tentacle has about seven single spines at regular intervals between the two rows of lateroabfrontal cells. Distally these spines are replaced at the same intervals by tufts of bristles. This might suggest that spines have evolved from bristles, or are at least homologous to them. *E. bilabiata* also has occasional longer, finer, abfrontal bristles which are separate from the spines and bristle clumps, and which are perhaps sensory in function. At each tentacle tip is a group of bristles between two spines. *Rhynchozoon* sp. possesses one or two clumps of bristles on each tentacle tip, as well as small spines or coarse bristles that are regularly spaced medially on each abfrontal surface. In *H. brunnea* between each pair of adjacent heavy spines there is a single long cilium. Although this is usually held straight and still, it is capable of movement. At the tip of each tentacle is a clump of fine bristles and a single very long cilium.

Tentacle elongation. It is difficult to imagine autocleaning by *H. hyalina*, with its short tentacles. One of the preadaptations to autocleaning behavior was an elongation of the tentacles. Tentacle elongation is here defined as L/w where L is tentacle length and w is width at the base of the tentacle. The tentacle elongation of *H. hyalina* is 17; that of *E. bilabiata* is 36; that of *H. brunnea* is 27 for equitentacled polypides and 29-52 for obliquely truncate polypides. Ryland (1975) showed a strong positive correlation between increasing lophophore diameter D and increasing tentacle length L, and concluded that D and L are interrelated measures of polypide size. Winston's (1979, Table 1) measurements showed that there is much less variation in w than in L among bryozoans; therefore, there is an increase in tentacle elongation with increasing polypide size. This means that, among the Ascophora, it was not until zooids had reached a cer-

TABLE 1. Prevalence of flattening the lophophore to form a disk and writhing in marine Bryozoa. The number of species in which behavior has been studied is given in parentheses.

Taxon	Behavior	Colony Type	Colony Currents	Source
Order Cheilostomata				
Suborder Ascophora (28)				
Family Petraliidae				
Coleopora gigantea	FLD	1,3	M	Winston 1979
F. Schizoporellidae				
Schizoporella floridana	W	4	S	Winston 1978
F. Eurystomellidae				
Eurystomella bilabiata	W	3	S	Winston 1979
F. Reteporidae				
Phidolopora pacifica	W	2	S	Winston 1979
Rhynchozoon sp.	FLD	5	S	Present study
Reteporellina evelinae	W	2,7	S	Winston 1978
F. Celleporidae				
Holoporella (Celleporaria) brunnea	W,FLD	5	S	Winston 1979 Present study
Holoporella albirostris	W,FLD	3,6,7	S	Winston 1978
Celleporina hassali	FLD	5	M	Winston 1978
Suborder Anasca (31)				
Family Lunulariidae				
Discoporella umbellata depressa	FLD	3,6,7	S	Winston 1978
F. Epistomiidae				
Synnotum aegyptium	W	2	W	Winston 1978
F. Bicellariellidae				
Bugula stolonifera	W	2	S	Winston 1978
F. Cribrilinidae				
Jullienula (Lyrula) hippocrepis	FLD	4	S	Winston 1979
Order Ctenostomata (13)				
F. Pherusellidae				
Pherusella brevituba	FLD	1,4	M	Winston 1979
Order Cyclostomata (9)				
F. Tubuliporidae				
"Tubulipora" sp.	W	6	M	Winston 1978

Key to Table 1. **Behavior:** FLD = flattening lophophore to form a disk; W = writhing.

Colony Type: 1 = behavior individualized; 2 = colony skeleton separates polypides, colony current generally unidirectional; 3 = polypides form temporary clusters, not reflected in skeletal morphology; 4 = polypides form fixed clusters, not reflected in skeletal morphology; 5 = polypides form fixed clusters, reflected in skeletal morphology, patterning irregular; 6 = polypides form permanent clusters enhanced by regular patterning of zooecium; 7 = polypides have some form of group action.

Colony Currents: W = weak; M = medium; S = strong.

tain size that they developed tentacles long and flexible enough for autocleaning to be mechanically feasible.

Occurrence of Autocleaning

Holoporella brunnea exhibits autocleaning and writhing behavior in response to strong or continued stimulation. Writhing is the penultimate response before complete retraction. The two responses are possibly related, since they both involve incomplete retraction and touching the tentacles to the colony surface.

Table 1 summarizes the occurrence of writhing and "flattening the lophophore to form a disk" from Winston's (1978, 1979) tables and from my own observations. Winston's "flattening the lophophore to form a disk" appears to be what I have ob-

served as incomplete autocleaning motions. Winston (pers. comm.) did not observe polypides to flatten their lophophores onto the colony surface as in autocleaning.

Of 28 ascophorans whose behavior has been studied, 9 flatten the lophophore (including autocleaning), or writhe, or both. Of 31 anascans that have been studied, only 4 show one trait or the other. Of 13 ctenostomes and 9 cyclostomes, only 1 species of each shows one trait or the other. Thus, flattening the lophophore and writhing are much more prevalent in the Ascophora than in other major gymnolaemate and stenolaemate groups. Within the Ascophora, the traits seem especially prevalent in the Reteporidae and Celleporidae. Also, these traits occur predominantly in species of Type 3 or greater colony organization which are able to produce strong colonial water currents.

Discussion

Evolution of Autocleaning

The ancestral ascophoran was probably a small, encrusting species like *Hippothoa hyalina.* If we assume a gradual increase in size in the descendants of the primitive ascophoran (a valid assumption because most ascophorans are larger than *H. hyalina*), one consequence would be a change in ejection capability, for two reasons. First, the primitive ascophoran, like *H. hyalina,* ejected large particles by tentacular downswing probably coordinated with a strong upward current produced by ciliary reversal (Fig. 5A). With an increase in zooid size, any forces exerted by the lophophore increaseed only as the square of linear lophophore measurements while the mass of particle increase as the cube of its radius. At some point, a zooid size was reached at which an ejection mechanism reliant upon lophophoral force was no longer effective. Second, due to increased tentacle elongation, the polypide was no longer able to retract quickly out from under a particle as does *H. hyalina* (Fig. 5A). When *Eurystomella bilabiata* is stimulated with a probe and attempts to retract rapidly, the extremely elongated tentacles flatten and drag on the colony surface, greatly slowing retraction. During normal retraction, the tentacles twist together to form a stiff clockwise spiral around the lophophore axis. Strangely, when the lophophore base has reached orifice level during retraction, the polypide spirals into the cystid with a counterclockwise twist. The twisting sequence is reversed as the polypide everts. This mechanism apparently functions to eliminate tentacle drag during normal retraction and is an indication that tentacle drag was indeed a problem.

When ascophorans became too large to employ the primitive methods of large-particle ejection, a slow response like the rolling motion of *E. bilabiata* (Fig. 5B) came to be employed. At this point, the ancestor was still at the individual level (Type 2 or 3) of integration.

The next significant step in the evolution of autocleaning came with a tightening of the lophophore sheet, which produced a more integrated colony with a strong, colony-wide water current. A polypide partially retracting to eliminate a large particle opened a temporary hole in the sheet, and the strong excurrent flow through the hole carried the particle away. (This actually occurs in *Holoporella brunnea* (Fig. 5C).) Once this happened, colonies in which polypides retracted as far as possible during ejection so as to remove themselves from the excurrent flow may have had a selective advantage.

At the last stage in the evolutionary process, the ascophoran ancestor employed strong excurrent flow in its ejection response and retracted to the colony surface, where its preadapted bristles or spines advantageously loosened bits of material and settled larvae that were also carried away by excurrent flow. A strong selective pressure would have existed for an increase in the size and stiffness of the spines, for the development of the means to retract and move them, and for the coordination of complex tentacular motion with partial polypide retraction to produce rasping. Why some living, non-autocleaning species such as *E. bilabiata* have spines is a puzzle. I speculate that spines may have evolved from bristles even before autocleaning, and that their original function might have been to remove debris from around the orifice during polypide eversion. This could certainly be the case in species that have a long peristome that accumulates debris.

Characteristics of Bryozoan Behavior

Bryozoan behavior is characterized by definite reaction forms, or reflexes, as defined by Brown (1975). Ejection, autocleaning, and writhing are generally attributable to definite stimuli. That an action is a reflex does not mean it is invariably elicited by the same stimulus, or that a given stimulus invariably elicits the same reflex, as was strongly emphasized by Jennings (1906). The manner in which an organism reacts depends upon its internal state, which in turn is influenced by past stimuli received and past reactions given.

Reactions in which a succeeding phase is determined by the previous one, albeit with some variability, are called chain reflexes (Jennings 1906). The behavioral patterns described in the present study are examples of this type of behavior. Within each species, there exist complexes of behavior, each complex containing several levels of response to different levels of stimulus. Thus, for example, *Holoporella brunnea* shows three distinct complexes of behavioral traits related to particle elimination: rejection, ejection, and autocleaning. Within each complex, there are two or more levels of response depending 1) upon the severity of the stimulus and 2) which stimuli and responses have immediately preceded a particular stimulus. A steady stream of tiny, sorted particles exits the lophophore via the ciliary rejection tract during normal feeding. Particles too numerous or large to exit in this manner cause the rejection tentacles to be moved ventrolaterally, widening the gap between them. If this does not eliminate the stimulus, then a simple ejection response and finally even flinging may be performed. Successive applications of a stimulus may therefore cause progression not only within a complex, but also from one behavioral complex to another. The concept of a complex of chain reflexes is well illustrated by the progression of *H. brunnea* from no response to repeated autocleaning, and finally to repeated writhing, under continuous exposure to bright light, or by the progression of *E. bilabiata* from simple ejection to flinging, and finally to "rolling" under continued stimulus from a large particle.

Bryozoan species display a number of behavior complexes. Ejection and rejection behavior seem to be present universally in all species whereas autocleaning and writhing seem to be limited. The number of behavioral traits present in different species varies—*H. hyalina* shows two types of ejection response, *E. bilabiata* three. Also, the degree of development of behavioral traits varies—*E. bilabiata* has much greater motility of the rejection tentacles than any other species I have observed.

This study has indicated that zooid behavior, zooid morphology, and colony integration are interrelated by bryozoans, and none can be fully understood without reference to the others. Bryozoans show many behavioral traits and complexes of traits other than those considered in this paper. It is this diversity and organized complexity of bryozoan behavior which allows productive application of a comparative approach.

Acknowledgements

Dr. Donald P. Abbott kindly made available laboratory space and equipment at the Hopkins Marine Station. Dr. Lars Silen, University of Stockholm, graciously read an earlier draft of this work and provided much encouragement. Dr. June R. P. Ross, Western Washington University, contributed many valuable technical and editorial suggestions.

Literature Cited

Borg, G. 1926. Studies of recent cyclostomatous Bryozoa. Zool. Bidr. Upps. 10: 181-507.

Brown, J. L. 1975. The Evolution of Behavior. W. W. Norton & Co., New York.

Bullivant, J. S. 1968. The method of feeding of lophophorates (Bryozoa, Phoronida, Brachiopoda). N. Z. J. Mar. Freshwat. Res. 2: 135-146.

Gordon, D. P. 1974. Microarchitecture and function of the lophophore in the bryozoan *Cryptosula pallasiana*. Mar. Biol. 27: 147-163.

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York.

Ryland, J. S. 1970. Bryozoans. Hutchinson University Library, London.

———. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. In: Proc. 9th Europ. Mar. Biol Symp. (H. Barnes, ed.), pp. 363-393. Aberdeen University Press, Aberdeen.

———. 1976. Physiology and ecology of marine bryozoans. Adv. Mar. Biol. 14: 285-443.

Winston, J. E. 1978. Polypide morphology and feeding behavior in marine ectoprocts. Bull. Mar. Sci. 28: 1-31.

———. 1979. Current-related morphology and behaviour in some Pacific Coast bryozoans. In: Advances in Bryozoology (G. P. Larwood and M. B. Abbott, eds.), pp. 247-267. Academic Press, London.

Received February 14, 1983
Accepted for publication July 1, 1983

Don Minore

USDA Forestry Sciences Laboratory
3200 Jefferson Way
Corvallis, Oregon 97331

Vaccinium Membranaceum Berry Production Seven Years After Treatment to Reduce Overstory Tree Canopies[1]

Abstract

Five overstory treatments were applied to a berry field near Mount Hood, Oregon, that was shaded by conifer forest. Big huckleberry (*V. membranaceum*) berry production was highest where 2,4-D applied to stem incisions (frills) reduced the overstory canopy without disturbing *vaccinium* shrubs in the understory. Production was lower where both overstory and understory were disturbed by cutting and burning or where the overstory canopy was not reduced.

Introduction

Big huckleberry (*Vaccinium membranaceum* Dougl. ex. Hook.) bears palatable berries that are extensively harvested by berry pickers in the Cascade Range of Oregon and Washington. Most of the berries are produced in sparsely forested subalpine areas where wildfires created favorable environmental conditions. Berry production declines when open-grown *V. membranaceum* shrubs become heavily shaded by closed forest canopies, however, and dense subalpine forests have seriously reduced huckleberry production in several heavily-used berryfields. In the absence of wildfire, silvicultural treatments to reduce or eliminate the forest overstory are necessary if former levels of berry production are to be restored.

Five overstory treatments were applied in 1974 to a berryfield shaded by dense young conifer forest, and subsequent berry production was compared to determine which was most effective. Treatment results after three years were published previously (Minore *et al.* 1979). Seven-year results are presented here.

Study Area

The study area was 11 km southwest of Mount Hood in Oregon on a gently sloping western aspect at an elevation of 1463 m in the Pacific silver fir (*Abies amabilis*) Forest Zone (Franklin and Dyrness 1973). Abundant *V. membranaceum* shrubs that covered about 45 percent of the area were overtopped by a conifer overstory of about 14,000 conifer trees per hectare that had an average canopy density of about 55 percent. Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) was the dominant species in this overstory; but Douglas-fir (*Pseudotsuga mensiesii* (Mirb.) Franco), noble fir (*Abies procera* Rehder), subalpine fir *A. lasiocarpa* (Hook.) Nutt.), grand fir (*A. grandis* (Dougl. ex D. Don) Lindl.), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), western hemlock (*T. heterophylla* (Raf.) Sarg.), Western white pine *Pinus monticola* Dougl.

[1]This paper reports research involving an herbicide. It does not contain recommendations for its use nor does it imply that the uses discussed here have been registered. All herbicides must be registered by appropriate state and/or federal agencies before they can be used.

ex. D. Don), Englemann spruce (*Picea engelmannii* Parry ex Engelm.), and Western red cedar (*Thuja plicata* Donn.) were also present above the *Vaccinium* shrubs. Beargrass (*Xerophyllum tenax* (Pursh) Nutt.) was dominant below the shrubs, but the herb stratum was also characterized by dwarf bramble (*Rubus lasiococcus* Gray), pearly everlasting (*Anaphalis margaritacea* (L.) B. & H.), and coiled pedicularis (*Pedicularis contorta* Benth.). The soil was coarse-textured, shallow, rocky, and low in nutrients.

Methods

The study consisted of a completely random experimental design, with five treatments replicated four times (Table 1). Square 0.14 hectare plots surrounded by 3 m buffer strips were arranged in a 4 x 5 plot grid. In the first treatment, all trees were cut on four randomly selected plots in 1973, and the resulting slash was broadcast-burned in late August 1974. The slash fire did not consume the blackened *Vaccinium* shoots, but it severely disturbed all understory vegetation.

A one-to-one mixture of 2,4-D amine and water was applied to stem incisions (frills) cut around the circumference of every tree larger than 5-cm d.b.h. on four other plots in early July 1974, when the last remnants of a heavy winter snow pack were melting and *Vaccinium* shrubs were just beginning to produce leaves. The frills were spaced 3.8 cm apart. About 50 percent of the 14,000 trees/hectare were large enough to treat. The overstory was severely disturbed, but the understory was undisturbed in this second treatment.

On a third series of plots, all vegetation below a height of 3 m was sprayed with a low volatile ester of 2,4-D in late July 1974 to dry the vegetation for subsequent burning. Burning was unsuccessful, however, and this became a 2,4-D spray treatment that slightly disturbed the overstory and moderately disturbed the understory. Cooperating pathologists inoculated the fourth series of plots with *Phellinus weirii* (Murr.) Gilbertson at this time by placing *P. weirii* cultures in contact with the roots of 25 well-spaced trees on each plot. Little or no overstory disturbance occurred on the *Phellinus* plots. The four control plots were not disturbed in any way. Beginning in 1975, berry pro-

TABLE 1. Treatments and their effects on overstory and understory vegetation.

Treatment	Overstory	Understory
Cut and burn	Destroyed	Crowns killed
2,4-D frill	>5-cm DBH killed	Undisturbed
2,4-D spray	Foliage below 3 m killed	Foliage killed
Phellinus weirii inoculation	Undisturbed	Undisturbed
Control	Undisturbed	Undisturbed

duction was sampled every other year on every treatment by picking and weighing all the berries on 16 systematically spaced .004-ha subplots on each of the 20 plots. *Vaccinium membranaceum* berries ripened irregularly on individual shrubs, and ripeness varied among treatments, so picked weights were converted to ripe weights:

$$\text{Ripe weight} = \frac{(\text{Picked weight})\ (\text{Average weight of a ripe berry})}{(\text{Average weight of a picked berry})}$$

The ripe weights were subjected to analyses of variance. Where significant differ-

ences among treatments occurred, Scheffe' (1959) multiple comparison tests were used to compare individual treatment means. Sample years were not compared statistically.

Results and Discussion

Meteorological influences are very important in determining annual huckleberry production (Minore and Dubrasich 1978), and the weather was more favorable for berry production in 1979 than it was in 1981 (Fig. 1). Nevertheless, the 2,4-D frill treatment

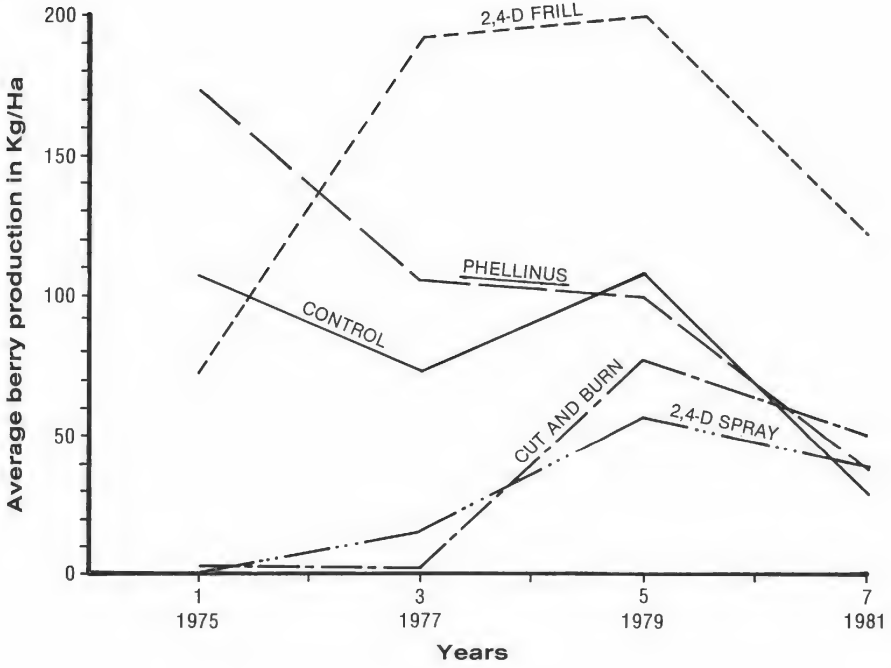

Figure 1. Average berry production trends during the 7 years after treatments were applied. Weather was unfavorable for berry production in 1981. The 1975 and 1977 data are from Minore, Smart and Dubrasich (1979).

produced more berries than other treatments in both years (Table 2). Indeed, the superiority of 2,4-D frilling became more evident each year. Scheffe' tests indicate that 2,4-D frill was significantly better than the average of all other treatments, but not significantly different than any single treatment at $P < 0.05$ in 1979. In 1981, berry

production of the 2,4-D frill treatment was significantly higher ($P < 0.05$) than all other treatments; the 2,4-D frill treatment was significantly higher than both *Phellinus* and control treatments at $P < 0.01$.

The increase in berry production on the 2,4-D frill plots occurred when treated overstory trees died; most of the overstory shade was eliminated without disturbing the understory *Vaccinium* shrubs. Similar results probably could be obtained by girdling the overstory trees. After either treatment, the dead trees remain standing for a long time. Only a few fell over during the seven years after 2,4-D treatment, and they have not limited access or created safety hazards. The overstory trees treated in this study were short, however, with diameters of less than 36 cm (14 in.). Leaving large dead trees on the stump would probably be hazardous.

TABLE 2. Average berry production, by treatment and year.[2]

Treatment	1979[3]	1981[4]
	Kg/ha	
2,4-D frill	200.1	122.6_a
Cut and burn	76.7	51.7_{ab}
2,4-D spray	57.2	38.5_{ab}
Phellinus inoculation	99.2	37.0_b
Control	108.0	29.9_b

[2]Each average is based on 4 replicates, with 16 subplot samples per replicate.

[3]Scheffe' tests showed the production on 2,4-D frill plots to be significantly higher ($P < 0.05$) than that of all other treatments in the frill vs. others comparison, but differences among individual treatments were not statistically significant.

[4]Averages within the bracket were not significantly different at $P < 0.05$ when compared with Scheffe' tests. Those followed by the same letter were not significantly different at $P < 0.01$.

None of the overstory died as a result of *Phellinus weirii* inoculations, and the *Phellinus* plots were indistinguishable from untreated control plots seven years after treatment. Inoculation failure or a prolonged delay in the expression of disease symptoms may be responsible.

The 2,4-D spray treatment, originally intended to facilitate overstory removal through subsequent burning, failed to affect overstory density significantly when the burning failed. *Vaccinium* shrubs were normal in appearance five years after being damaged by 2,4-D. Seven years after treatment, their berry production was similar to that of other *Vaccinium* shrubs shaded by a dense overstory.

Vaccinium shoots were killed by fire on the cut and burn plots in 1974. Although they resprouted vigorously, the *Vaccinium* shrubs had not completely recovered from this disturbance after seven years.

The failure of fire to improve *Vaccinium membranaceum* berry production in seven years is surprising, for most huckleberry fields seem to have become established after wildfires, and periodic fires probably eliminated the forest overstories that shaded huckleberry shrubs in the past. Huckleberry recovery from fire (Miller 1977, 1978) varies both with fire intensity, fuel condition, soil moisture, burning season, and *Vaccinium* species, however. Postburn recovery of *V. globulare* can be exceedingly slow in Western Montana (Stickney 1981).

Past increases in *Vaccinium membranaceum* berry production associated with the burning of overstory trees and huckleberry shrubs in the Cascade Range must have been delayed until long after the fires. Reestablishment of overstories also occurred long after the fires when uncontrolled fildfires swept over large areas, however; and the delay probably was not particularly important when burns of all ages were readily available to the huckleberry pickers of former years. The delay may be important now. If the results obtained on the study site are applicable elsewhere in the Pacific silver fir zone, the elimination of forest overstories by girdling or herbicide-frill treatments that do not disturb the *Vaccinium* understories may be the most feasible way to increase huckleberry production rapidly in heavily used berry fields recently overgrown by subalpine forest.

Literature Cited

Franklin, Jerry F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Report PNW-8. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Miller, Melanie. 1977. Response of blue huckleberry to prescribed fires in western Montana larch-fir forest. U.S.D.A. For. Serv. Res. Papaer INT-188. Interm. For. and Range Exp. Stn., Ogden, Utah.

———. 1978. Effect of growing season on sprouting of blue huckleberry. USDA For. Serv. Res. Note INT-240. Interm. For. and Range Exp. Stn., Ogden, Utah.

Minore, Don and Michael E. Dubrasich. 1978. Big huckleberry abundance as related to environment and associated vegetation near Mount Adams, Washington, USDA For. Serv. Res. Note PNW-322. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

———. Minore, Don, Alan W. Smart, and Michael E. Dubrasich. 1979. Huckleberry ecology and management research in the Pacific Northwest. USDA For. Serv. Gen. Tech. Report PNW-93. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Scheffé, H. 1959. The Analysis of Variance. Wiley, New York.

Stickney, Peter F. 1981. Vegetative recovery and development. *In* Clearcutting and fire in the larch/Douglas-fir forests of western Montana—a multifaceted research summary (N.V. DeByle, ed.). USDA For. Serv. Gen Tech. Report INT-99. P. 33-40. Interm. For. and Range Exp. Stn., Portland, Oreg.

Received March 7, 1983
Accepted for publication June 23, 1983

Daniel E. Wujek

Department of Biology
Central Michigan University
Mt. Pleasant, Michigan 48859

James L. Wee

Department of Botany and Plant Pathology
Michigan State University
East Lansing, Michigan 48224

New, Rare, and Unusual Algae from Montana

Abstract

A checklist of taxa previously unreported or infrequently reported as occurring in Montana is presented. The 163 species and varieties include those in the Rhodophyta (1), Xanthophyta (4), Chlorophyta (5), Chrysophyta (11), and the largest group, Bacillariophyta (142).

Introduction

This checklist has been prepared to extend the freshwater algal flora of Montana. The first published reference to Montana algae appeared in 1891 (Anderson and Kelsey). In the following year, Dr. T. F. Allen identified three charophytes from a Montana pond (Williams 1892). Since these first two reports, a number of other papers pertaining to the Montana algal flora have been published. This literature was reviewed and brought up to date through 1977 by Prescott and Dillard (1979). Bahls (1981, 1982) made further additions to the diatom flora. One checklist of freshwater algae near this area (British Columbia: Stein 1975) has also appeared, part of an overall study of the freshwater algae of British Columbia (see also Stein and Gerrath 1968, 1969).

As a contribution to a continuing effort to expand knowledge of the state's algal flora, the present report lists, in annotated form, species and varieties rarely reported or previously unreported as occurring in northwest Montana. In an area that is ecologically well suited to support a diverse algal flora, few representative taxa have been reported. While many of the species included in this paper are known to have a cosmopolitan distribution, the need for complete phytogeographical data justifies placing them on record in Montana.

It is noteworthy that some of the species listed here are reported previously only from northern European and Alaskan stations. Their appearance in Montana, therefore substantiates their north temperate distribution. Although many forms, have a wide and very general range, numerous species seem to fall into either latitudinal or longitudinal zonations (Prescott and Croasdale 1942).

Material and Methods

Field collections from Flathead, Lake, Lincoln, Glacier, and Missoula counties (Table 1) were made during the summer of 1976 and 1977, examined live, or preserved (5 percent formalin or a few drops of 1 percent $0s0_4$) in the laboratory. The collections

TABLE 1. Algae collecting sites in northwest Montana. The number after each collecting site is used to identify locations for each taxon in the checklist.

Flathead County
- Bitterroot Lake (1)
- Echo Lake (2)
- Egan Slough (3)
- Foy Lake (4)
- Hungry Horse Reservoir (5)
- Lake of the Woods (6)
- Little Bitterroot Lake (7)
- McDonald Lake (8)
- Shaws Slough (9)
- Smith Lake (10)
- Swan Pond (11)
- Swan River (12)
- Yellow Bay (Flathead Lake) (13)

Glacier County
- Cleveland Hanging Bog (14)
- Saint Mary Lake (15)

Lake County
- Black Lake (16)
- Lake Mary Ronan (17)
- Lost Creek (18)
- Jette Lake (19)
- Mission Reservoir (20)
- Mission Wells Pond (12)
- Ninepipe Reservoir (22)
- Pablo Reservoir (23)

Lincoln County
- Crystal Lake (24)
- Dickey Lake (25)
- Lake Koocanusa (26)
- Loon Lake (27)
- Murphy Lake (28)
- Thomson Lake, Lower (29)

Missoula County
- Lake Alva (31)
- Lake Inez (32)
- Seeley Lake (33)
- Summit Lake (34)

were made from over 30 ponds, lakes, streams, oxbows and ephemeral ponds (Fig. 1). Electron micrographs for identification of taxa belonging to the Mallomonadaceae were prepared from material air-dried on stubs for scanning electron microscopy (SEM) and coated with gold in either a Hummer I sputter coater or a Varians vacuum evaporator. Observations were made with a JEOL-35 or an AMR-1200 SEM. For transmission electron microscopy (TEM), material was air-dried on Formvar coated grids and examined in a Philips EM 300. Diatoms were acid cleaned and mounted in Hyrax (Wujek 1966). Light photomicrographs were made on Kodachrome 25 or Panatomic X film using a Zeiss microscope (bright field, phase contrast, Nomarski interference contrast). Preserved material, diatom slides, and light and electron micrographs documenting this report are deposited in the herbarium of Central Michigan University (CMC) or in the private collections of the authors.

Nomenclature and taxonomic arrangement within the checklist follow that of Prescott (1962), Patrick and Reimer (1966), Bourrelly (1966, 1968) and Ettl (1978). For each taxon, the location from which the collection was made is indicated by a number (specific county localities are listed in Table 1). Systematic notes and habitat distribution notes are given where appropriate.

Chrysophyta

Mallomonadaceae

Chrysosphaerella brevispina Lauterborn (1)[1]
C. longispina Lauterborn emend Nicholls (11)
Mallomonas actinoloma Asmund & Takahashi (26)
M. papillosa Harris & Bradley (25)
M. pumilo Harris & Bradley (28)

[1]See Table 1 for specific location corresponding to number(s).

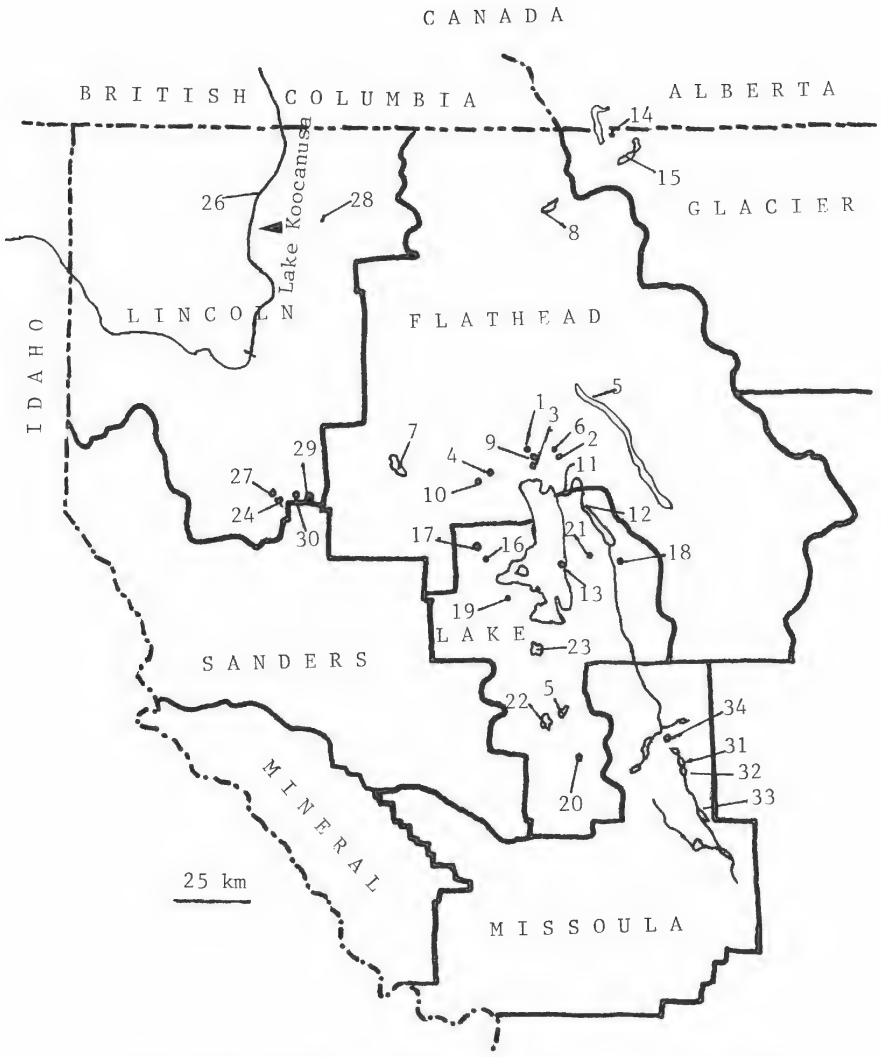

Figure 1. Location of sampling sites. See Table 1 for names of specific collecting sites.

Paraphysomonas vestita (Stokes) de Saedeler (1)
Synura echinulata Korsh. (7)
S. petersenii Korsh. (17)

Ochromonadaceae

Epipyxis utriculus Ehr. (31)

Chrysococcaceae

Biocoeca lacustris Clark (18)

Lepochromulina calyx Scherf (34)
Genus previously reported for North America by Stein (1975).

Chlorophyta

Characiaceae

Actidesmium hookeri Reinsch (20)

Chlorangiaceae

Stylosphaeridium stipitatum Geitl. & Gimesi (19)

Coleochaetaceae

Coleochaete divergens Pringsheim (34)

Tetrasporaceae

Paulschulzia pseudovolvox (Schulz) Skuja (6,12)

Volvocaceae

Pledorina californica Shaw (19)

Xanthophyta

Botryochloridaceae

Ducelliera chodatii (Ducella.) Teil. (34)
Colonial colorless alga. Considered by some authors to be a phycomycetous fungus, perhaps in the Saprolegniales (Kusel-Fetzman and Novak 1981).

Gloeobotrydaceae

Chlorobotyrs ellipsoidea (Pasch.) Bourrelly (5)

Neonemataceae

Neonema quadratum Prascher (21)

Tribonemataceae

Bumilleriopsis brevis Printz (34)

Rhodophyta

Batrachospermaceae

Batrachospermum ectocarpum Sirodot (13)
Attached to rocks at 24 m depth.

Bacillariophyta

Coscinodiscaceae

Cyclotella striata (Kütz.) Grun. (34)
Stephanodiscus subtilis (Van Goor) A. Cl. (8)

Rhizosoleniaceae

Rhizosolenia curvata (Kütz.) Grun., ex Rabh. (3)

Diatomaceae

Diatoma anceps v. *linearis* M. Perag. (6)
D. Hiemale v. *hiemale* (Roth) Heib. (13)
Denticula pelagia v. *intermedia* Hust. (34)
D. subtilis Grun. (14)
D. tenuis v. *crassula* (Naeg.) Hust. (8,12,34)

Fragilariaceae

Asterionella formosa Hassall (3,8,12,32,34)
Fragilaria constricta Ehr. (32)
Synedra amphicephala Kütz. v. *amphicephala* (8)
S. filiformis v. *exilis* Cl. (21)
S. minuscula Grun. v. *minuscula* (3)
S. rumpens v. *familiaris* (Kütz.) Grun. (6,21)
S. ulna v. *chaseana* Thomas (8)
S. ulna v. *longissima* (W. Sm.) Grun. (8,32)
S. ulna v. *obtusa* V. H. (21)

Eunotiaceae

Eunotia fallax A. Cl. (34)
E. flexuosa v. *eurycephala* Grun. (21)
E. incisa W. Sm. ex Greg. v. *incisa* (34)
E. monodon Ehr. (3)
E. naegelii Migula (11,12,21)
E. tenella (Grun.) Cl. (34)
E. valida Hust. (12,13)
E. vanheuckii v. *intermedia* (Krasske ex Hust.) Patr. (21,34)

Achnanthaceae

Achnanthes hauckiana Grun. v. *hauckiana* (22)
A. lanceolata v. *omissa* Reim. (32)
A. lapidosa Krasske (14)
A. laterostrata Hust. (32)
A. linearis (W. Smith) Grun. (32,34)
A. marginulata Grun. (32)
A. peragallii Brun. & Herib. (32)
A. plonensis Hust. (34)

Naviculaceae

Anomoeoneis vitrea (Grun.) Ross v. *vitrea* (3,6,8,34)
Caloneis alpestris (Grun.) Cl. (14)
C. ventricosa v. *minuta* (Grun.) Patr. (8)
C. ventricosa v. *truncatula* (Grun.) Meist. (8,34)

Diploneis marginestriata Hust. v. *marginestriata* (14)
D. oblongella (Naeg. ex Kütz.) Ross (22)
Mastogloia grevillei W. Sm. (34)
Navicula americana v. *moesta* Temp. & Perag. (14)
N. amphibola Cl. (3,21)
N. biconica Patr. v. *biconica* (32)
N. canalis Patr. v. *canalis* (22)
N. caroliniana Patr. v. *caroliniana* (4)
N. cincta (Ehr.) Ralfs (19,21)
N. gottlandica Grun. (8)
N. halophila (Grun.) Cl. (4)
N. heufleri Grun. v. *heufleri* (8)
N. ilopangeoensis Hust. v. *ilopangoenesis* (6)
N. lacustris Greg. v. *lacustris* (14)
N. latelongitudinalis Patr. v. *latelongitudinalis* (21)
N. menisculus Schum. v. *menisculus* (8)
N. modica Hust. (34)
N. mournei Patr. v. *mournei* (34)
N. mutica v. *cohnii* (Hilse) Grun. (8,34)
N. mutica v. *tropica* Hust. (3)
N. mutica v. *ventricosa* (Kütz.) Cl. (8)
N. notha Wallace (4)
N. paludosa Hust. (19)
N. plausibilis Hust. (8)
N. protracta Grun. v. *protracta* (13,32)
N. rhombicula Hust. v. *rhombicula* (21)
N. rhynchocephala Kütz. (21)
Frustulia rhomboides v. *capitata* (A. Mayer) Patr. (12,14,19,34)
F. rhomboides v. *crassinervia* (Breb. ex W. Sm.) Ross (12,34)
F. rhomboides (Shr.) DtT. v. *rhomboides* (12)
F. vulgaris (Thwaites) DeT. v. *vulgaris* (34)
Neidum affine v. *longiceps* (Greg.) Cl. (34)
N. bisulcatum (Lagerst.) Cl. v. *Bisulcatum* (34)
N. iridis (Ehr.) Cl. v. *iridis* (32)
Pinnularia abaujensis v. *rostrata* (Patr.) Patr. (32)
P. acuminata v. *bielawskii* (Herib. & Perag.) Patr. (14)
P. braunii v. *amphicephala* (A. Mayer) Hust. (34)
P. dactylus Ehr. v. *dactylus* (34)
P. divergens v. *bacillaris* (M. Perag.) Mills (12)
P. divergens W. Sm. v. *divergens* (12)
P. flexuosa Cl. v. *flexuosa* (19)
P. gibba v. *mesogongyla* (Ehr.) Hust. (21)
P. gibba v. *parva* (Ehr. Grun. (34)
P. intermedia (Lagerst.) Cl. v. *intermedia* (34)
P. mesolepta v. *angusta* Cl. (34)
P. obscura Krasske v. *obscura* (8)
P. polyonca (Breb.) O. Mull. v. *polyonca* (21)

P. stomatophora (Grun.) Cl. v. *stomatophora* (34)
P. subcapitata Greg. (8,14,34)
P. torta (Mann.) Patr. v. *torta* (34)
P. viridis v. *minor* Cl. (34)
Stauroneis fluminea Patr. & Freese v. *fluminea* (32)

Gomphonemataceae

Gomphonema acuminatum v. *pusilla* Grun. (19,21,32,34)
G. affine Kütz. v. *affine* (3,11,14)
G. affine v. *insigne* (Greg.) Andrews (13)
G. angustatum v. *citera* (Hohn & Hellerm.) Patr. (13)
G. angustatum v. *intermedia* Grun. (8)
G. angustatum v. *sarcophagus* (Greg.) Grun. (8,21,34)
G. brebissonii Kütz. v. *brebissonii* (14)
G. consector Hohn & Hellerm. v. *consector* (6,8,21)
G. dichotomum Kütz. (6)
G. grunowii Patr. v. *grunowii* (21)
G. septum Mogh. v. *septum* (13,34)
G. subclavatum (Grun.) Grun. v. *subclavatum* (14)
G. subtile v. *sagitta* (Schum.) Cl. (34)
G. tenellum Kütz. v. *tenellum* (3,6,11)
G. truncatum v. *capitatum* (Ehr.) Patr. (19,21,34)
G. truncatum Ehr. v. *truncatum* (3,6,11,19,32,34)

Cymbellaceae

Amphora ovalis v. *affinis* (Kütz.) V. H. ex DeT. (6,14,19)
A. perpusilla (Grun.) Grun. (8,32)
Cymbella angustata (W. Sm.) Cl. v. *angustata* (8,14,21)
C. cymbiformis v. *nonpunctata* Font. (8)
C. heteropleura v. *subrostrata* Cl. (14)
C. inaequalis (Ehr.) Robin. v. *inaequalis* (14,34)
C. lunata W. Sm. v. *lunata* (3,12,14,19,21,32,34)
C. minuta v. *latens* (Karaske) Reim. (8,14)
C. minuta Hilse ex Rabh. v. *minuta* (3,8,12,13,14,19,32,34)
C. minuta v. *pseudogracilis* (Choln.) Reim. (12)
C. minuta v. *silesiaca* (Bleisch ex. Rabh.) Reim. (8)
C. muelleri Hust. v. *muelleri* (21)
C. prostrata v. *auerswaldii* (Rabh.) Reim. (21,34)
C. rupicola Grun. v. *rupicola* (3)
C. subaequalis Grun. v. *subaequalis* (8)

Epithemiaceae

Epithemia adnata v. *minor* (Perag. & Herib.) Patr. (3,19)
E. adnata v. *porcellus* (Kütz.) Patr. (21,33,34)
E. adnata v. *probosidea* (Kütz.) Patr. (11,21)
E. argus v. *alpestris* Grun. (12,32,34)

E. turgida v. *westermanii* (Ehr.) Grun. (34)
Rhopalodia musculus (Kütz.) O. Mull. v. *musculus* (14,19)
R. parallela (Grun.) O. Mull. v. *parallela* (32)

Nitzchiaceae

Hantzschia amphioxys v. *capitata* O. Mull. (8,12,34)
H. amphioxys (Hantz.) Grun. v. *vivax* (8)
H. elongata (Hantz.) Grun. (32,34)
Nitzschia flexa Schum. (8,34)
N. frustulum v. *perpusilla* (Rabh.) Grun. (19)
N. ignorata Krasske v. *ignorata* (32)
N. invisitata Hust. v. *invisitata* (34)
N. thermalis Kütz. (19,21)
N. vivax W. Sm. (32,34)

Surirellaceae

Campylodiscus clypeus Ehr. v. *clypeus* (16)
C. noricus v. *hibernicus* (Ehr.) Grun. (3)
Cymatopleura elliptica (Breb.) W. Sm. v. *elliptica* (32)
Surirella biseriata v. *constricta* Grun. (32)
S. linearis v. *constricta* (Ehr.) Grun. (32)
Stenopterobia intermedia Lewis v. *intermedia* (34)

Acknowledgements

We would like to thank Dr. John Tibbs, Director of the University of Montana Biological Station, for his assistance and the the use of the station's facilities. Individuals who have assisted us in various aspects of the study include: Michael Chapo, Meredith Welling, Erich Weber, and Michael Graebner. We are indebted to Michael Weis for his photographic assistance and to Julia Nickolaus for the illustration.

Literature Cited

Anderson, F. W. and F. D. Kelsey. 1981. Common and conspicuous algae Montana. Bull. Torrey Bot. Club 18:137-146.
Bahls, L. L. 1981. Diatoms of Lewis and Clark Caverns. Proc. Mont. Acad. Sci. 40:11-18.
———. 1982. Eight new diatom genus records for Montana. Proc. Mont. Acad. Sci. 41:7986.
Bourrelley, P. 1966. Les Algues d'eau Douce. Tome I. Algues Vertes. Editions N. Boubee & Cie, Paris.
———. 1968. Les Algues d'eau Douce. Tome II. Les Algues Jaunes et Brunes. Editions N. Boubee & Cie, Paris.
Ettl, E. 1978. Susswasser von Mitteleuropa. Band 3, Teil. Xanthophyceae. G. Fischer Verlag, Stüttgart.
Kusel-Fetzmann, E. and H. Nouak. 1981. *Ducellieria chodati*-algae oder pilz? Pl. Syst. Evol. 138: 199-207.
Patrick, R. and C. W. Reimer. 1966. The Diatoms of the United States. Acad. Nat. Sci. Philadelphia Monograph 13.
Prescott, G. W. 1962. Algae of the Western Great Lakes Area. Wm. C. Brown Co., Dubuque, Iowa.
——— and H. T. Croasdale. 1942. The algae of New England. II. Amer. Midl. Nat. 27:662-676.
——— and G. E. Dillard. 1979. A checklist of algal species reported from Montana 1981 to 1977. Monograph No. 1, Proc. Mont. Acad. Sci. 38:1-102.
Stein, J. R. 1975. Freshwater algae of British Columbia: the Lower Frazer Valley. Syesis 8:119-184.
——— and J. F. Gerrath. 1968. Freshwater algae of British Columbia: desmids of bog lakes in Coast Mountain area. Syesis 1:187-197.
——— and ———. 1969. Freshwater algae of British Columbia: The Queen Charlotte Islands. Syesis 2:213-226.

Williams, R. S. 1892. The flora of a Montana pond. Bull. Torrey Bot. Club 19:192-194.
Wujek, D. E. 1966. Seasonal variation in number and volume of plankton diatoms. Trans. Amer. Micros. Soc. 85:541-547.

Received March 28, 1983
Accepted for publication October 12, 1983

Thomas J. Loranger

and

David F. Brakke

Institute for Watershed Studies
Western Washington University
Bellingham, Washington 98225

Temperature Characteristics, Annual Heat Storage, and River Diversion Influence on a Monomictic Lake

Abstract

The mean annual change in heat storage in Lake Whatcom was determined to be 23,100 cal cm^{-2} $year^{-1}$. Isotherm development in one basin of the lake occurs independently of the other two basins; a shallow sill separating it from the rest of the lake appears to be the major isolating factor. River water diverted into the lake at the rate of 2.31×10^5 m^3 day^{-1} had negligible effects on total heat storage in the lake.

Introduction

Biochemical cycling in lakes is regulated by temperature and density gradients. Consequently, knowledge of heat structure and content in lakes is an important aspect of limnology. Much of the literature dealing with lentic thermal structure and heat flux, published in North America, has been concerned with dimictic lakes influenced by a continental climate (Birge and Juday 1914, Hutchinson 1957, Stewart 1973, Blanton 1973). Less literature is available concerning monomictic lakes, particularly those influenced by a maritime climate.

A temperature and heat content inventory is provided for Lake Whatcom, in the Puget Sound Lowland of Washington State. Data on isotherm and thermal profile development are presented for the entire lake as well as for individual basins within the lake. The heat content of the lake was calculated as a Birgean heat budget. In 1962 a portion of the Nooksack River was diverted into Lake Whatcom; the effect of this cool diversion water on lake heat structure was negligible.

Location

Lake Whatcom is located 29 km south of the Canadian border in western Washington State. The east-west axis of the lake lies at 48°43′ N. latitude; the north-south axis lies at 122°20′ W. longitude. Lake Whatcom is 95 m above mean sea level.

Methods

The Institute for Watershed Studies at Western Washington University provided data for the study of Lake Whatcom. From 1962 until 1972 and from 1979 until 1981, physical and chemical data were recorded at 5 m depth levels from five major sampling stations on the lake. These data were recorded weekly. Temperature was recorded with a thermistor calibrated with a standard thermometer. Temperature data used in annual

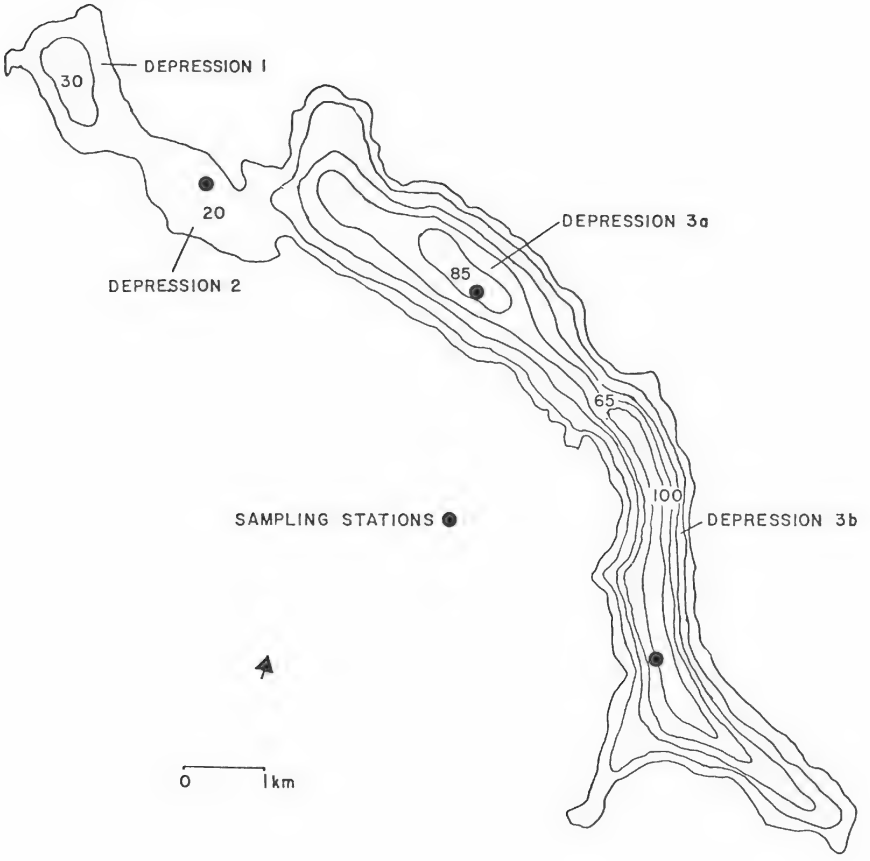

Figure 1. Morphometry of Lake Whatcom.

heat budget calculations represent mean water column temperatures taken from three sampling stations located at representative locations on the lake (Fig. 1). Basin to basin isotherm development, as well as mean epilimnetic and hypolimnetic temperatures, was determined in the lake. For ease of calculation, one year (1970) was chosen for these comparisons based on temperature profile development. Profile development during this year was representative of that during all other years of study.

The most widely accepted means of expressing heat content in lakes is by means of a Birgean heat budget (Hutchinson 1957). The amount of heat that would be released from Lake Whatcom upon cooling to 0°C was determined by: $\Theta_w = \sum_{Z_0}^{Z_m} t_z a_z h_z$, where Θ_w = heat content of the lake water in calories; z_0 = surface of the lake; z_m = maximum depth of the lake; t_z = average temperature in degrees celsius of a unit layer of water of thickness h_z (cm) with midpoint at depth z and a_z the area at depth

z (cm^2) (Wetzel and Likens 1979). Sufficent temperature data were available to calculate eight years of change in annual heat storage (Birgean heat budget) for Lake Whatcom.

The area of Lake Whatcom at each successive 5 m depth interval was determined by planimetry from a 1/24,000 scale contour map of the lake produced by Lighthart *et al.* (1972). Volumes of the lake were determined between each depth interval.

In 1962 a portion of the Middle Fork of the Nooksack River was diverted into Lake Whatcom, at the rate of 2.31 x 10^5 m^3 day^{-1}, for a six-month period to maintain water level and supply. Figures on diversion quantity were obtained from the city of Bellingham water treatment plant, for comparison with heat storage fluctuation in the lake.

Results and Discussion

Morphometry

Lake Whatcom has a surface area of 20 km^2. The lake has a maximum depth of 100 m and a mean depth of 45 m, with a total volume of 8.948 x 10^8 m^3. The lake has three major depressions (Fig. 1). Depression 1 is located at the north end of the lake and has a maximum depth of approximately 30 m. Depression 2 is separated from depression 1 by a sill 5 m in depth; depression 2 has a maximum depth of approximately 20 m. Depression 3 dominates the central and southern portion of the lake and contains 95 percent of the lake's volume; it is separated from depression 2 by a sill 10 m in depth and has a maximum depth slightly over 100 m.

Thermal Stratification

Lake Whatcom reaches maximum thermal stratification by mid-August. A distinct metalimnion was consistently present by June 1 in each year. In 1970, at the time of maximum thermal discontinuity, the depth to the thermocline was approximately 17 m. The lakewide mean temperature was found to be 10.9° C at the time of maximum thermal discontinuity in August (1963, 1966-1972). The lakewide mean epilimnetic temperature for this period was 15.9° C, and the mean hypolimnetic temperature (below 25 m) was 6.7° C.

Basin to Basin Comparisons

Thermal profile development occurred simultaneously in the three major depressions of Lake Whatcom (1970). Depression 3, the deepest, has the largest difference between mean epilimnetic and hypolimnetic temperatures at the time of maximum thermal stratification (Fig. 2).

Isotherm evolution in Depression 1 occurred independently of the other two depressions. At the time of maximum thermal stratification in Depression 1, depth to the thermocline was greater and mean hypolimnetic temperatures were higher than in the other two depressions (Fig. 2). Depressions 1 and 2 have very similar morphometries with volumes of 19.4 m^3 x 10^6 and 18.0 m^3 x 10^6, respectively (Lighthart *et al.* 1972). The shallow sill between the two depressions (5 m deep) determines the independent nature of isotherm formation in depressions 1 and 2 (Fig. 3). The sill between depressions 2 and 3 is approximately 10 m deep. A prevailing southerly wind promotes mixing between basins, but is limited mainly to effects of basin 3 on basin 2. Mixing

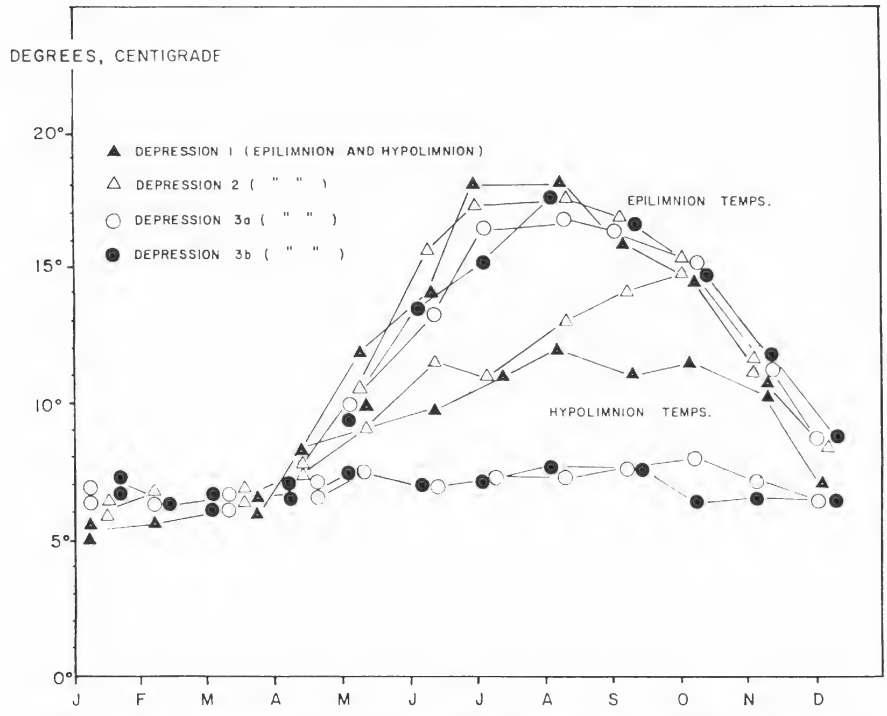

Figure 2. Mean water column temperatures of the epilimnion and hypolimnion in the three basins of Lake Whatcom, 1970.

is compounded by a 2.3 x 10^5 m^3 daily water withdrawal from the hypolimnion of Depression 2 for supply to the city of Bellingham.

Birgean Annual Heat Budgets

Birgean annual heat budgets (change in annual heat storage) of Lake Whatcom were calculated for eight separate years. The mean maximum heat storage for the eight years of study was 49,400 cal cm^{-2} $year^{-1}$. The mean minimum winter heat storage for the study years was 26,300 cal cm^{-2} $year^{-1}$. The resulting mean annual change in heat storage for the eight-year period was 23,100 cal cm^{-2} $year^{-1}$. By comparison, we have calculated a Birgeon heat budget for Lake Washington of 21,000 cal cm^{-2} $year^{-1}$ (Loranger and Brakke 1983). At 28.85 x 10^8 m^3, Lake Washington has a significantly greater volume than Lake Whatcom, as a result there is greater total heat storage in Lake Washington. The deeper water column of Lake Whatcom, however, permits greater total heat storage per cm^2 of lake surface and promotes a larger heat budget in the lake. In temperate lakes that are sufficiently deep to maintain hypolimnetic temperatures near 4° C year round, Birgean heat budgets usually vary between 30,000 to 40,000 cal cm^{-2} $year^{-2}$ (Wetzel 1975). Very few lakes have heat budgets in excess of 50,000 cal cm^{-2} $year^{-1}$. In temperate latitudes, Birgean annual heat budgets are strongly correlated with lake mean depth, area, and volume, rising continuously with lake dimensions

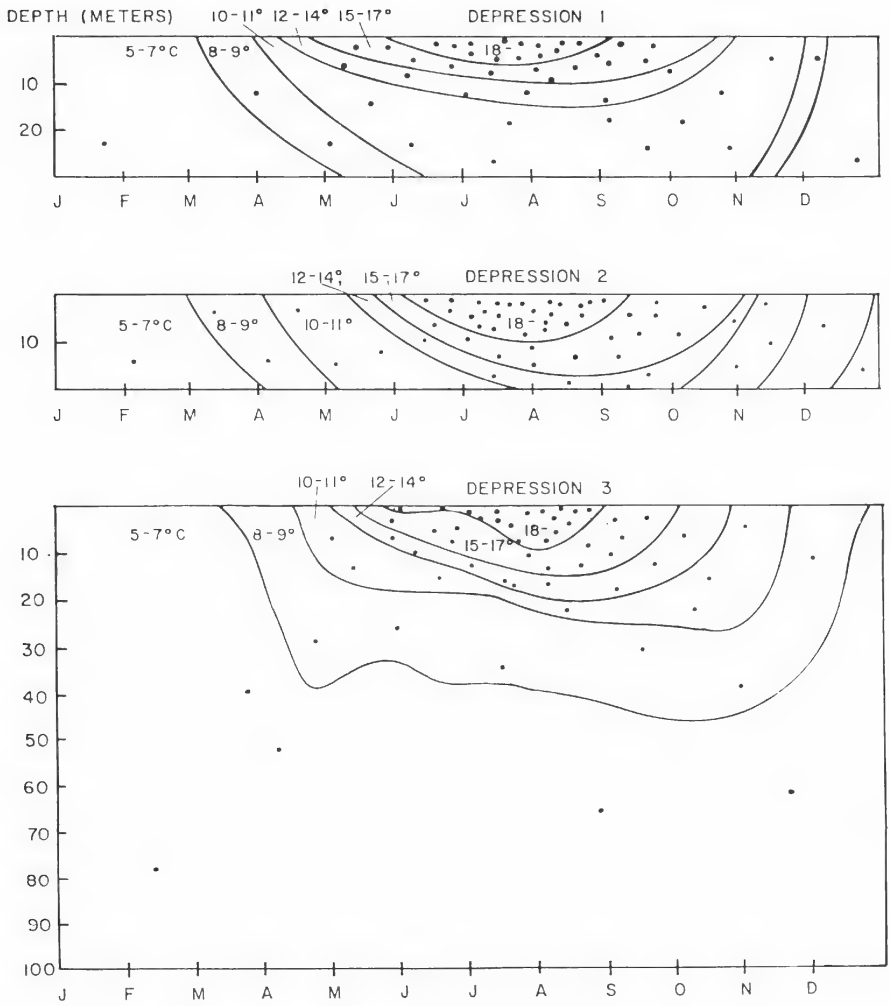

Figure 3. Isotherm evolution, 1970.

(Gorham 1964). Dimictic lakes tend to exhibit higher changes in mean annual heat storage than monomictic lakes of similar size.

Diversion Water Influence on Heat Storage

Beginning in 1962, water from the Nooksack River was diverted into Lake Whatcom at the south end of Depression 3b (Fig. 1), to counteract water use by the city of Bellingham and industrial uses, and to stabilize lake level. The Nooksack River water is diverted at the rate of 2.31×10^5 m^3 day^{-1}. The diversion gates are usually opened in the spring, when the lake level begins dropping, and closed again in the fall. Warmer, dryer years often require more total days of diversion.

The river water is cooler than the mean water temperature of Lake Whatcom. In January and February the river water cools to 5° C and in August it is often near 11° C. This large volume of cool diversion water input could be a factor in depressing heat storage in Lake Whatcom. The maximum amount of diversion time before mid-August, in any year to date, has been five months. This translates into 34.0 x 10^6 m^3 of river water. Using 8° C as a conservative spring mean diversion water temperature and 10.9° C as the lakewide mean temperature at the time of maximum heat storage, the mean temperature of the lake would be lowered to 10.79° C. In terms of heat storage, this amounts to a loss of 503 cal cm^{-2}. Stewart (1973) showed that in three mid-western lakes of moderate size (mean depth of 15 m) and moderate heat budgets (25,000 cal cm^{-2} $year^{-1}$), there could be a 2,000 to 3,000 cal cm^{-2} fluctuation in heat storage in two days time during summer months. In light of this, a heat loss of 503 cal cm^{-2} in a water column with 48,150 cal cm^{-2} in storage is an insignificant amount.

Stewart (1973) showed that power plant thermal discharge input to Lake Monoma (Wisconsin) that could theoretically cycle the entire volume of the lake (105 x 10^6 m^3) in one year, had at most localized effects on heat structure and had negligible effects on total heat storage in the lake. He concluded that diurnal variations in temperature appear to have a much greater effect on total heat storage in the lake than any anthropogenic thermal inputs. Similarly, cool water influx from river diversion in Lake Whatcom appear to have little more than localized effects on heat structure in basin 3 of the lake.

Conclusion

Lake Whatcom was found to have reached maximum thermal discontinuity by mid-August. Lakewide mean temperature at maximum thermal discontinuity was 10.9° C. Thermal profile development occurred simultaneously in the three major depressions of Lake Whatcom. Isotherm evolution in Depression 1 occurred independently of evolution in the other two depressions; the shallow sill separating Depression 1 from the rest of the lake appeared to be the major isolating factor. The lake was found to have a mean annual Birgean heat budget of 23,100 cal cm^{-2} $year^{-1}$ (eight-year mean).

Diversion of the Nooksack River into Lake Whatcom was found to have a negligible effect on heat storage in the lake. The maximum amount of water diverted into Lake Whatcom before 1 August in any year was 34 x 10^6 m^3. This volume of water caused a 0.11° C drop in lakewide temperature at the time of maximum heat storage in the lake.

Literature Cited

Blanton, J. O. 1973. Some comparisons in the thermal structure of Lakes Wood, Kalamalka, Okanogan, Shaha, and Osoyoos, British Columbia. J. Fish. Res. Bd. Canada, 30:917-925.

Gorham, E. 1964. Morphometric control of annual heat budgets in temperate lakes. Limnol. Oceanogr. 9:525-529.

Hutchinson, G. E. 1957. A Treatise on Limnology, v. 1. John Wiley and Sons, New York.

Lighthart, B., G. F. Kraft, and C. J. Flora. 1972. The limnology of Lake Whatcom. I. Morphometry. Inst. for Freshwater Studies, Western Washington University, Tech. Rep. 15.

Loranger, T. and D. F. Brakke. 1983 (in review). Morphometric control of annual heat budgets and thermal structure evolution in two monomictic lakes.

Stewart, K. H. 1973. Detailed time variations in mean temperatures of some Madison lakes. Limnol. Oceanogr. 18:218-225.

Wetzel, R. G., and G. E. Likens. 1979. Limnological Analysis. Saunders, Philadelphia, London, Toronto.

Received June 27, 1983
Accepted for publication October 2, 1983

TABLE 1. Volume at depth, Lake Whatcom.

Depth Interval (m_v)	Volume (m3)	Percentage of Total Volume
0-5	9.517 x 107	10.6%
5-10	8.659 x 107	9.7%
10-15	7.717 x 107	8.6%
15-20	6.908 x 107	7.7%
20-25	6.559 x 107	7.3%
25-30	6.163 x 107	6.9%
30-35	5.812 x 107	6.5%
35-40	5.522 x 107	6.1%
40-45	5.237 x 107	5.8%
45-50	4.929 x 107	5.5%
50-55	4.520 x 107	5.0%
55-60	3.476 x 107	4.4%
60-65	3.387 x 107	3.8%
65-70	2.898 x 107	3.2%
70-75	2.464 x 107	2.7%
75-80	1.958 x 107	2.2%
80-85	1.434 x 107	1.6%
85-90	1.013 x 107	1.1%
90-95	.542 x 107	.6%
95-100	.380 x 107	.4%
Total Volume—89.481 x 107		100%

TABLE 2. Maximum and minimum temperature profiles, Whatcom, 8-year mean, (63, 66-72).

	Lake Whatcom	
	Mean temperature at contour interval	
	max	min
0.5	20.2	6.1
5-10	19.7	5.9
10-15	18.1	5.9
15-20	14.4	5.9
20-25	10.4	5.9
25-30	8.2	5.9
30-35	7.5	5.9
35-40	7.0	5.9
40-45	6.8	5.9
45-50	6.6	5.9
50-55	6.6	5.9
55-60	6.5	5.9
60-65	6.5	5.9
65-70	6.5	5.9
70-75	6.4	5.9
75-80	6.4	5.8
80-85	6.4	5.8
85-90	6.3	5.8
90-95	6.3	5.8
95-100	6.3	5.7

TABLE 3. Comparative volume and isotherms at depth, Lake Whatcom.

Depth	Whatcom % volume	Isotherm at max. depth of interval
0-10	20.5	18° C
10-15	8.5	14.5° C
15-20	7.5	10.5° C
20-25	7.5	8.0° C
25-100	6.6	6.0° C

TABLE 4. Yearly totals of Nooksack River diversion to Lake Whatcom.

Year	Total days of Diversion	Total m3 diverted
1962	180	41.5 x 106
1963	270	62.3 x 106
1964	231	53.3 x 106
1965	225	51.9 x 106
1966	237	54.7 x 106
1967	195	45.0 x 106
1968	108	24.9 x 106
1969	180	41.5 x 106
1970	204	47.1 x 106
1971	120	27.7 x 106
1979	219	50.5 x 106

Richard L. Knight[1]

Wildlife Science Group
University of Washington
Seattle, Washington 98195

Dwight G. Smith

Department of Biology
Southern Connecticut State University
New Haven, Connecticut 06515

David M. Gaudet

Fisheries Research Institute
University of Washington
Seattle, Washington 98195

and

Albert W. Erickson

Wildlife Science Group
University of Washington
Seattle, Washington 98195

Nesting Ecology of Mourning Doves in Fruit Orchards in North-Central Washington

Abstract

Nesting ecology of Mourning Doves (*Zenaidura macroura*) was studied in three orchard types which received differing levels of human management and contained trees of differing fruit type, age, and growth-form. The orchard receiving only moderate levels of human management had the highest density of nesting doves. Pruned, apple-standard trees between 20 and 27 years old were the preferred nest trees, presumably because of the abundance of horizontal limbs for nest sites. The peaks of nesting and nesting success occurred during July. Nesting success was highest in the cultured orchard, much lower in the semi-cultured orchard, and zero in the feral orchards, with these differences attributed mainly to the differing levels of human activity. Nesting success was highest in the older, apple-standard trees, and lowest in the non-apple fruit trees and younger, apple-dwarf trees. The average number of young produced per pair varied from none to 3.1.

Introduction

Harris *et al.* (1963) and Caldwell (1964), among others, have noted that Mourning Doves (*Zenaidura macroura*) show nest site preferences for certain tree species. Oliver (1966) and Zeigler (1977) suggested that fruit type, age, and growth-form of fruit trees are important factors in dove nest site selection in orchards. To our knowledge, no one has studied Mourning Dove nesting ecology in orchards receiving different levels of management. This paper compares the nesting ecology of Mourning Doves in three markedly different orchard types (cultured, semi-cultured, and feral) and examines

[1]Present address: Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53076.

differences in nesting densities and nesting success with fruit type, age, and tree growth-form of fruit trees.

Study Area and Methods

Field work was conducted in four orchards located within 14 km of each other along Rufus Woods Lake, a 72-km stretch of the Columbia River between Chief Joseph and Grand Coulee dams in Okanogan and Douglas counties. The region is largely uncultivated land, typical of the arid shrub-steppe regions of eastern Washington and is used for cattle grazing with small areas in orchards, grain, and hay. Erickson *et al.* (1977) have presented a detailed physiographic, vegetative, and faunal description of the area.

The four orchards chosen for study differed in size, fruit type, age, and tree growth-form (Table 1), as well as in the amount of human management administered. Tree growth-form refers to tree shape and was either "standard" or "dwarf." The cultured orchard (Chief Joseph) was a commercial orchard which was mowed, pruned, treated with pesticides, irrigated (ground sprinklers and rill irrigation), and harvested. The semi-cultured orchard (Thalhimer's) received little attention other than irrigation (ground sprinklers) and occasional pruning. The feral orchards (Mulberry and Goldmine homestead orchards) had received no human treatment for 40 to 50 years.

Each orchard was checked a minimum of once per week for Mourning Dove nesting activity in 1975: Chief Joseph Orchard (CJO) was checked 23 times between 6 April and 29 August, Thalhimer's Orchard (TO) was checked 18 times between 5 April and 11 August, and Mulberry (MHO) and Goldmine (GHO) homestead orchards were both visited 30 times between 5 April and 26 July. Because of the small size of TO and the two feral orchards (Table 1), all trees were checked during each visit. The size of CJO made checking every tree prohibitive; therefore, a predetermined number of randomly selected trees were checked (Table 1).

Nests were examined with a car mirror attached to a long pole and were checked until their fates were determined. Nesting terminology is as follows: a nesting attempt was determined by the presence of eggs or adults on a nest; a successful nesting attempt was one that fledged at least one young; a destroyed nest was one which was no longer present during a later visit or one evidencing mortality of eggs or young. The approximate nesting population of each stand was determined by using the largest number of active nests located in a single day (McClure 1942). Lowe (1956) suggested that this method probably underestimates the actual nesting population as it is not likely that all pairs will have a nest active at any one time.

Results and Discussion

Orchard and Nest Tree Utilization

Overall nesting density was highest in TO, indicating that the semi-cultured orchard type offered the most attractive nesting situation for doves (Table 2). Fichter (1959) in Idaho, and Zeigler (1977) in Washington, suggested that Mourning Dove nesting density was the result of both nesting cover and surrounding habitat requirements such as food and water. TO and CJO were equidistant from abundant water (i.e. Columbia River) and food (i.e. grain fields) yet TO had a much higher nesting density than CJO in fruit tree types of similar age and growth form (Table 2). One possible explanation for this difference was the different levels of human activity in the two orchards.

TABLE 1. Tree characteristics of three orchard types sampled for Mourning Dove production in 1975.

Fruit type and growth-form	Date stand planted	Size of stand (ha)	Average height of stand (m)	Average DBH of stand (cm)	Number of trees sampled	Percent of total stand sampled
Cultured Orchard						
(Chief Joseph)						
apple, standard	1955	8.7	5.5	25.4	859	27.5
apple, standard	1960	2.4	5.3	25.4	205	23.2
apple, dwarf	1960	2.7	4.6	25.4	302	21.8
apple, dwarf	1970	2.5	3.0	10.2	357	21.2
apple, dwarf	1971	0.5	3.0	10.2	146	42.6
apple, dwarf	1972	1.2	2.1	5.1	146	18.6
cherry, standard	1965	0.8	6.0	17.8	222	66.7
pear, standard	1965	1.2	4.8	15.2	269	30.9
Semi-cultured Orchard						
(Thalhimer)						
apple,standard	1948	0.6	5.4	25.4	76	100.0
prune, standard	1948	0.1	no data	no data	32	100.0
cherry, standard	1948	0.04	no data	no data	5	100.0
pear, standard	1948	0.04	no data	no data	14	100.0
Feral Orchards						
(Mulberry Homestead)						
apple, standard	1910	0.1	7.8	15.2	40	100.0
mulberry, standard	1910	0.1	11.1	33.0	41	100.0
(Goldmine Homestead)						
apple, standard	1895	0.2	7.2	22.9	21	100.0

TABLE 2. Tree availability and usage by Mourning Doves in three orchard types, 1975.

Fruit type, growth-form, and age of tree	Percent of total trees in orchards	Ranking of fruit tree abundance	Number of nesting attempts	Number of nesting attempts per 100 trees checked	Ranking of dove usage
Cultured Orchard					
(Chief Joseph)					
apple, standard, 20	32.4	1	76	8.8	2
apple, standard, 15	9.2	4	12	5.9	3
apple, dwarf, 15	14.4	3	10	3.0	5
apple, dwarf, 5	17.5	2	3	0.8	7
apple, dwarf, 4	3.6	7	1	0.7	8
apple, dwarf, 3	8.1	6	0	0.0	9
cherry, standard, 10	3.5	8	3	1.4	6
pear, standard, 10	9.0	5	2	0.7	8
Total or average	97.7		107	4.3	
Semi-cultured Orchard					
(Thalhimer)					
apple, standard, 27	0.8	9	14	18.4	1
prune, standard, 27	0.3	12	0	0.0	9
cherry, standard, 27	0.1	13	0	0.0	9
pear, standard, 27	0.1	13	0	0.0	9
Total or average	1.3		14	11.0	
Feral Orchards					
(Mulberry and Goldmine)					
apple, standard, 65-80	0.6	10	2	3.3	4
mulberry, standard, 65	0.4	11	0	0.0	9
Total or average	1.0		2	2.0	
Grand total or average	100.0		123	4.5	

CJO was under intensive and continual human management whereas TO was attended sporadically during the nesting season. Other than our visits, the feral orchards were never visited by humans, yet, they had virtually no nesting doves. Although both feral orchards were close to water, they were surrounded by extensive shrub-steppe which provides a less-rich food source than do grain fields (Zeigler 1977). Two alternative explanations for the lower nesting density in the feral orchards could be interspecific nest-site competition (which appeared low in CJO and TO where few other bird species nested), and the reduced suitability as nest sites of the unpruned, and therefore, extremely dense canopied, trees (see below).

The highest Mourning Dove nesting densities occurred in 20- and 27-year-old apple-standard trees (Table 2). Lowest nesting densities occurred in non-apple fruit trees such as cherry, pear, mulberry, and prune trees, as well as in apple-dwarf trees less than 5 years old. There was a nonsignificant relationship between ranking of fruit tree abundance and ranking of fruit tree usage by nesting doves (Daniels' correlation, $D = 198$, $P > 0.4$), indicating that doves showed nest tree preferences.

Harris *et al.* (1963) found that doves preferred nest sites on horizontal limbs that offered an unobstructed flight path. Coon *et al.* (1981) demonstrated that the probability of a nest succeeding was affected by its structural stability which in turn was influenced by its placement. Nests placed on horizontal limbs are probably more secure than those placed on sloping limbs. Results from nesting studies in eastern Washington orchards (summarized in Zeigler 1977) indicated that highest nesting densities occurred in pruned 25-30-year-old apple-standard trees which had large, flat horizontal limbs which are preferred as nest sites. Non-apple fruit trees and apple-dwarf trees less than 15 years old had the lowest nesting densities. These findings agree closely with our results. Non-apple fruit trees and young apple-dwarf trees lacked horizontal limbs. Oliver (1966) and Zeigler (1977) found 2½ times as many nests in 19-year-old apple-standard trees as in 14-year-old apple-dwarf trees, but equal nesting densities were found when the trees were 30 and 25 years old respectively, at which time the apple-dwarf trees had horizontal limbs. The unpruned 65-80-year-old apple-standard trees at GHO and MHO lacked horizontal limbs and unobstructed flight paths, which might partially explain the low nesting densities.

Nesting Season

Earliest and latest dates of active nests in CJO were 13 April and 29 August, respectively. A second nesting attempt was not located in CJO until the first week in May. Comparable dates for TO were 9 May and 27 July whereas earliest dates in the two feral orchards were 24 May and 22 June. Length of nesting season based on presence of active nests was 139 days in CJO and 80 days in TO. Nesting activity was high from May through August, peaking in July, during which 38 percent of all nests were found. The inclusive dates of nesting activity are similar to those reported in four Idaho orchards by Fichter (1959) who also observed a July peak.

Nesting Success

Nesting success increased from April through July and was correlated with the increase in number nesting attempts (Table 3). The relationship between number of nests and nesting success was significant ($\chi^2 = 8.8$, $df = 4$, $P < 0.05$).

Fichter (1959) observed that the number of young fledged per nesting attempt and

TABLE 3. Monthly distribution of Mourning Dove nesting attempts in apple trees for all orchards combined, 1975.

Month	Percent and number of total tests	Percent and number of nesting attempts successful
April	0.8 (1)	0.0 (0)
May	19.5 (24)	8.3 (2)
June	22.8 (28)	50.0 (14)
July	38.2 (47)	60.9 (28)
August	18.7 (23)	21.7 (5)
Total or average	100.0 (123)	40.1 (49)

the percentage of nesting attempts successful are useful parameters in interpreting Mourning Dove nesting studies. Fichter (*Ibid.*) summarized several studies and found that successful nesting attempts ranged from 47 to 71 percent, and that the number of young fledged per nesting attempt ranged from 0.85 to 1.38. In our study, differences between orchard types in percentage of nesting attempts successful ranged from zero to 67 percent and varied significantly with fruit type and age of tree ($\chi^2 = 12.5$, df = 8, $P < 0.05$) (Table 4). The percentage of nesting attempts successful was highest in the older apple-standard trees, and all nests were unsuccessful in the feral orchards and in non-apple fruit trees in all of the three orchard types. The average number of young fledged, per nesting attempt, ranged from zero to 1.3 in the various orchards and showed the same patterns as the percentage of nesting attempts successful (Table 4).

Of 107 nesting attempts in CJO, 33 (31 percent) failed from either weather or predation during the incubation stage and only one failed during the nestling stage. Of 196 eggs in all nests, 56 (29 percent) were destroyed by weather or predation, whereas, only three of 99 young (3 percent) disappeared. In TO ten of 14 nests (71 percent) were destroyed by either weather or predation during the incubation stage and none were lost during the nestling stage. Sixteen of 21 eggs (76 percent) were destroyed and no young were lost. Both nesting attempts in the feral orchards failed during the incubation stage. The percentage of eggs lost in CJO falls within the range of 22 to 46 percent summarized by Fichter (1959) but the percentage of eggs lost in TO is higher than previously reported. The percentage of nestlings lost in both CJO and TO is less than the range of 5 to 22 percent summarized by Fichter (*Ibid.*).

A large difference between the percentage of destroyed nesting attempts in CJO and TO (31 versus 71 percent) cannot be explained entirely by differences in weather or numbers of potential predators, as both orchards were similarly situated and had approximately equal numbers of domestic cats and nesting Black-billed Magpies (*Pica pica*) (Erickson *et al.* 1977). Why then should dove nests that occur in similar fruit tree types and orchards that are approximately similar in predator populations and other environmental variables such as weather, food, and water, differ markedly in both nesting densities and nesting success rates (Table 4)? We suggest that the differences in nesting densities and nesting success among similar fruit tree types in CJO and TO were largely the result of differences in levels of human activity. High and continual human activity in CJO may have disrupted nesting activities resulting in a lower nesting density and likewise disrupted potential predator activities resulting in higher nesting success. TO experienced only intermittent human activity, allowing less disruption of nesting and predator activity, which may explain the higher nesting density and lower

TABLE 4. Productivity of Mourning Doves in three orchard types, 1975

Fruit type, growth-form, and age of tree	Nesting pairs per 100 trees checked[a]	Nesting attempts per pair[b]	Percent nesting attempts successful	Eggs per nesting attempt	Percent eggs hatched	Percent young fledged	Young fledged per nesting attempt
Cultured Orchard							
(Chief Joseph)							
apple, standard, 20	3.3	2.6	47.4	1.8	53.6	86.7	0.9
apple, standard, 15	2.4	2.4	66.7	1.9	69.6	100.0	1.3
apple, dwarf, 15	1.0	3.3	30.0	1.8	33.3	100.0	0.6
apple, dwarf, 5	0.3	3.0	33.3	2.0	33.3	100.0	0.7
apple, dwarf, 4	0.7	1.0	0.0	2.0	0.0	0.0	0.0
apple, dwarf, 3	0.0	—	—	—	—	—	—
cherry, standard, 10	0.4	3.0	0.0	2.0	0.0	0.0	0.0
pear, standard, 10	0.7	1.0	0.0	0.0	0.0	0.0	0.0
Sample average	1.7	2.5	44.9	1.8	50.5	89.9	0.9
Semi-cultured Orchard							
(Thalhimer)							
apple, standard, 27	6.6	2.8	14.3	1.5	19.0	100.0	0.3
prune, standard, 27	0.0	—	—	—	—	—	—
cherry, standard, 27	0.0	—	—	—	—	—	—
pear, standard, 10	0.0	—	—	—	—	—	—
Sample average	3.9	2.8	14.3	1.5	19.0	100.0	0.3
Feral Orchards							
(Mulberry and Goldmine)							
apple, standard, 65-80	3.3	1.0	0.0	0.5	0.0	0.0	0.0
mulberry, standard, 65	0.0	—	—	—	—	—	—
Sample average	2.0	1.0	0.0	0.5	0.0	0.0	0.0
Grand average	1.8	2.5	40.7	1.8	47.2	90.3	0.8

[a]Based on largest number of active nests located in a single day.
[b]Total number of nesting attempts divided by the largest number of active nests located in a single day.

nesting success. Osborne and Osborne (1980) found that urban Blackbirds (*Turdus merula*) nesting near human activity had higher desertion rates and lower predation levels than nests farther from human activity. They implied that the frequency, intensity, and predictability of human activity influenced nesting success by altering desertion rates and predation levels.

Productivity

Average number of nesting attempts per pair of doves ranged from 1.0 to 3.3 in the three orchard types (Table 4).

Estimates from our study indicate that Mourning Doves produced an average between none and 3.1 young per pair depending on orchard type and fruit tree type. Harris *et al.* (1963) discussed the number of young per pair that should be produced by nesting doves to maintain a stable population and presented estimates between 3.2 and 4.6 young per pair, depending on annual mortality rates. Fichter (1959) summarized published findings and reported that the average number of young fledged per pair of doves ranged from 2.0 to 6.7. Productivity from the orchards we studied for one nesting season was near the low end of the published range.

Acknowledgments

We thank Robert A. McCabe, John R. Patterson, Stanley A. Temple, and Donald L. Zeigler for their criticisms of this paper. In addition, critical suggestions from two referees, E. G. Bizeau and I. O. Buss, improved the manuscript. The U.S. Army Corps of Engineers, Seattle, provided the financial assistance necessary for this study. We gratefully acknowledge the Colville Confederated Tribes for their support of our field studies. The assistance of Jim B. Athearn is appreciated. This study would not have been possible without the support of George and Clara Thalhimer, and the Weber, Berg, and Tim families.

Literature Cited

Caldwell, L. D. 1964. Dove production and nest site selection in southern Michigan. J. Wildl. Manage. 28:732-737.

Coon, R. A., J. D. Nichols, and H. F. Percival. 1981. Importance of structural stability to success of Mourning Dove nests. Auk 98:389-391.

Erickson, A. W., Q. J. Stober, J. J. Brueggeman, and R. L. Knight. 1977. An assessment of the impact on the wildlife and fisheries resource of Rufus Woods Reservoir expected from the raising of Chief Joseph Dam from 946 to 956 m.s.l. U.S. Army Corps Engin., Seattle, Washington.

Fichter, E. 1959. Mourning Dove production in four Idaho orchards and some possible implications. J. Wildl. Manage. 23:438-447.

Harris, S. W., M. A. Morse, and W. H. Longley. 1963. Nesting and production of the Mourning Dove in Minnesota. Amer. Midl. Nat. 69:150-172.

Lowe, J. I. 1956. Breeding density and productivity of Mourning Doves on a county-wide basis in Georgia. J. Wildl. Manage. 20:428-433.

McClure, H. E. 1942. Mourning Dove production in southwestern Iowa. Auk 59:64-75.

Oliver, W. 1966. A comparative dove nesting preference survey of semi-dwarf and standard apple trees in the Okanogan Valley, Washington. Wa. Dept. Game, Olympia, Washington.

Osborne, P., and L. Osborne. 1980. The contribution of nest site characteristics to breeding success among Blackbirds (*Turdus merula*). Ibis 122:512-517.

Zeigler, D. L. 1977. Evaluation of the breeding habitat of the Mourning Dove in eastern Washington. Wash. Dept. Game, Olympia, Washington.

Received February 23, 1983
Accepted for publication July 7, 1983

John T. Ratti
Wildlife Biology
Washington State University
Pullman, Washington 99164-4220

Selected Avian Systematic Problems in the Northwest: The 1983 A. O. U. Check-list

The sixth edition (1983) of the American Ornithologist's Union (A. O. U.) Check-list of North American Birds has recently been published and contains numerous systematic changes from the fifth edition (1957). The biological justification for such changes has been presented elsewhere (Mayr 1970, Selander 1971, Ratti 1980), and Arbib (1983) provided a general critique of the new Check-list. The purpose of this discussion is to consider several systematic problems with species in the Northwest that were not solved by changes in the new Check-list. In some cases, such problems were not addressed by the Committee on Classification and Nomenclature due to insufficient data prior to deadlines for revision and publication of the new Check-list. The 1983 edition does not present subspecies; consequently, discussion of subspecific populations will reference the 1957 Check-list edition.

Western Grebe (*Aechmophorus occidentalis*)

Two color morphs of Western Grebe, referred to as "light-phase" and "dark-phase" (Storer 1965, Ratti 1981) were originally described as separate species by George Lawrence (*in* Baird 1858:894-895). Lawrence named the dark form the Western Grebe (*Podiceps occidentalis*) and the light form Clark's Grebe (*P. clarkii*). However, they were later considered color phases of the same species (Coues 1874, Henshaw 1881) and A. O. U. (1886, 1931, 1957) classified the forms as a single species. Recent research has clearly disclosed that sympatric populations of these color morphs function as separate biological species (Ratti 1979, Nuechterlein 1981). Interbreeding (hybridization) occurs at a very low rate and isolating mechanisms have been identified. Regardless of this information, the new A. O. U. (1983) Check-list classifies only one *Aechmophorus* species, the Western Grebe. Arbib (1983:835) noted that "the [A. O. U.] committee has been alternately, even simultaneously, criticized for being too radical in its revisions and for being much too conservative." I feel this case is an example of being too conservative. Although existing data (prior to the 1983 revision) adequately addressed the criteria necessary for classifying the forms as two distinct species (Mayr 1963, 1970), recent research provides additional information important to this problem. Unpublished research (Alquist, Bledsoe, Ratti and Sibley) has revealed DNA differences between Western and Clark's grebes comparable to other closely related, but clearly distinct avian congeners. Ratti (1984) reports morphological differences between Western and Clark's grebes, especially with mandible morphology. Additional unpublished data (Ratti) supports the hypothesis by Nuechterlein (1981:344) that Western and Clark's grebes are ecologically segregated by feeding at different water depths (i.e.,

water depth niche partitioning). None of these later factors (e.g., DNA, morphology, niche) are primary criteria of the biological species concept, but such differences are consistent with those commonly observed for most closely related distinct species.

Harlan's Hawk (*Buteo jamaicensis harlani*)

The Harlan's Hawk has been subjected to several classification changes. The second edition of the A. O. U. (1895) classified Harlan's Hawk as a subspecies; in 1957 (A. O. U. 1957) this hawk was considered a distinct species, but was again assigned subspecific status in 1973 (A. O. U. 1973). The new Check-list (A. O. U. 1983) is consistent with the 1973 supplement and the Harlan's Hawk is considered a subspecies of the Red-tailed Hawk (*B. jamaicensis*). The present subspecific classification is based on reports of frequent interbreeding between *B. c. harlani* and other Red-tailed Hawk subspecies (Taverner 1927, Godfrey 1966, Lowe 1978). The taxonomic category of subspecies has three criteria: 1) discrete geographic range during reproductive periods, 2) phenotypic or morphological divergence, and 3) insufficient isolating mechanisms in zones of contact with other conspecific subspecies (Mayr 1970, Ratti 1980). Classification of *harlani* was based on criteria 2 and 3, and knowledge of a discrete geographic range did not exist. However, this problem has been solved by the recently published work of Mindell (1983). Mindell (1983:163) reports "The Alaskan breeding range found to be exclusive to Red-tailed Hawks of the *harlani* subspecies ran from Farwell at the east slope of the Alaskan range, north to Tanana and the Yukon River, west to Norton Sound, and south to St. Marys and Aniak." These data eliminate a previously existing problem and substantiate the subspecific status of the Harlan's Hawk.

Thayer's Gull (*Larus thayeri*)—Iceland Gull (*L. glaucoides*)

Although Thayer's and Iceland gulls are classified as distinct species, available biological evidence suggests that a systematic change is likely with a future A. O. U. Check-list supplement. A detailed taxonomic discussion of these closely related gulls (including the subspecies *L. g. kumlieni*) is presented by Weber (1981a). The A. O. U. (1983) classification of *L. thayeri* and *L. glaucoides* as separate species appears to be based largely on the research by Smith (1966). However, even Smith (1966:69-70) seems uncomfortable with his data regarding assortative mating between *thayeri* and *kumlieni*. Weber (1981a) also noted reservation with the data and analysis, and concluded that "his [Smith's] treatment of *kumlieni* and *thayeri* as different species is open to question." Weber (1981a) suspected greater rates of interbreeding between *kumlieni* and *thayeri* than indicated by existing data, and was "inclined to favor merging *thayeri* with *L. glaucoides*" (Weber 1931b). These suspicions are supported by Godfrey (unpublished data), whose field party, contrary to Smith (1966), found no evidence of assortative mating among individuals of the *thayeri-kumlieni* complex at Home Bay, Baffin Island, Northwest Territories. He now considers these taxa to be conspecific under *L. glaucoides* (W. E. Godfrey, pers. comm.).

Western Gull (*Larus occidentalis*)—Glaucus-winged Gull (*L. glaucescens*)

Hoffman *et al.* (1978) report extensive interbreeding and a high frequency of intermediate morphs in sympatric breeding populations of *L. occidentalis* and *L. glaucescens*.

However, they recommend continued recognition of *occidentalis* and *glaucescens* as distinct species due to hypothesized introgression stability by the two forms. Weber (1981b:81) disfavors the scenario offered by Hoffman *et al.* (1978) and believes there is "no convincing reason for assuming equilibrium in the hybrid zone;" he discusses evidence suggesting that the zone of contact "is imperceptibly being driven toward complete intergradation." Weber (1981b) also notes the very narrow interpretation of the biological species concept by Hoffman *et al.* (1978), and favors merging *L. glaucescens* with *L. occidentalis* to become *L. o. glaucescens.* The A. O. U. (1983:222) Check-list committee also appears uncomfortable with the present classification of *occidentalis* and *glaucescens* as distinct species and notes that "these two will probably prove to be conspecific."

An associated problem is the relationship of Western Gull subspecies, *L. o. occidentalis*, *L. o. wymani*, and *L. o. livens*. Weber (1981b) notes geographic isolation of *livens* from *wymani* and nominate *occidentalis*, and mentions clear morphological characters that separate *livens* from the latter two subspecies. He suggests that *livens* might be a distinct species (*L. livens*). Hand (1981) has disclosed distinct vocalization of *livens* and also believes *livens* should be classified as a separate species. LeValley (1980) has reported a similar conclusion based on his data that indicate *livens* to be distinct in color, morphology, and voice from *L. o. occidentalis* and *L. o. wymani.* These data indicate significant divergence by *livens*, but unfortunately, sympatric populations do not exist to examine the effectiveness of isolating mechanisms. However, available data do suggest that it may be appropriate to classify *livens* a superspecies, i.e., an allopatric population so different that effective isolating mechanisms are *assumed* to exist that would prevent interbreeding with closely related populations in sympatry. Mayr (1970) noted that over 30 percent of the breeding birds in North America meet the classification criteria of a superspecies.

Sapsuckers (*Sphyrapicus* spp.)

The 1983 A. O. U. Check-list classifies three sapsucker species, the Yellow-bellied (*Sphyrapicus varius*), Red-breasted (*S. ruber*), and Williamson's (*S. thyroideus*). *S. ruber* was previously considered a subspecies of *varius* (A. O. U. 1957). An additional subspecies, the Red-naped Sapsucker (*S. v. nuchalis*, A. O. U. 1957) may also be elevated to distinct species status with future revisions. Johnson and Zink (1983) studied sympatric nesting populations of *ruber*, *nuchalis*, and *thyroideus* in south-central Oregon and northeastern California. They report assortative mating between *ruber* and *nuchalis* and note that "although infrequent hybridization between *ruber* and *nuchalis* occurs, there is no evidence of either a hybrid swarm or of the species losing their phenotypic identity" (Johnson and Zink 1983:881). Johnson and Zink (1983) conclude that the Red-naped Sapsucker (*nuchalis*) is specifically distinct.

Western Flycatcher (*Empidonax difficilis*)

The Western Flycatcher has three designated subspecies (A. O. U. 1957), two of which breed in northwestern states. *E. d. difficilis* occurs along the Pacific Coast, and *E. d. hellmayri* occurs throughout the interior highlands; their range is reported to be sharply divided by the Cascade Mountains (Johnson 1980). Johnson (1980:111) reports that "in view of their [*difficilis* and *hellmayri*] profound differences in size, color, and

voice, these groups approach the species-level of differentiation." However, this conclusion is complicated by limited evidence of interbreeding by sympatric populations in the Siskiyou region of northern California. Johnson (1980) acknowledges that additional research is needed to resolve this problem, but prefers to consider *hellmayri* a "megasubspecies." Johnson uses this term to reference subspecies approaching species status. Mayr (1970) classifies such cases as "semispecies"; i.e., populations that have acquired some attributes of species rank but remain borderline cases between species and subspecies. Future research must concentrate on the sympatric populations in the Siskiyou region to more clearly examine rates of interbreeding and potential isolating mechanisms.

Northwestern Crow (*Corvus caurinus*)

The A. O. U. (1983) Check-list acknowledges that the Northwestern Crow and American Crow (*C. brachyrhynchos*) are closely related, and they are classified superspecies (defined above). A. O. U. (1983:509) also notes that *caurinus* and *brachyrhynchos* are "considered conspecific by some authors." This particular systematic controversy is especially difficult. Unlike most superspecies, zones of sympatry between *caurinus* and *brachyrhynchos* do exist, but field identification is a difficult problem. Northwestern and American crows are phenotypically very similar, and are separated primarily by voice, habitat, behavior, and morphology. Unfortunately, these factors are subject to variation and interpretation, and field identification is much less discrete than with other closely related species having distinct recognizable phenotypic characteristics. Consequently, it is difficult to obtain a large number of field observations on hybridization rates. Johnston (1961) studied the relationship between *caurinus* and *brachyrhynchos*, and has concluded that the forms are conspecific. Johnston (1961:31) studied voice patterns in Washington and reported:

a. Birds of extreme mid-southwestern Washington and those east of the Cascades are of the *hesperis* [voice] type [i.e., *C. b. hesperis*, A. O. U. 1957].
b. Birds of the Olympic Peninsula, mid- and probably much of northwestern Washington are of intermediate voice types, sometimes resembling *caurinus* and sometimes *hesperis*.
c. Birds of the San Juan Islands, and perhaps from this locality northward, are of the *caurinus* [voice] type.

Johnston (1961) also studied habitat use and measurements, and based on evidence of intergradation, considers the Northwestern Crow a subspecies of the American Crow, and recommends calling the Alaska and coastal British Columbia crows *C. b. caurinus*, those in Washington west of the Cascade range intermadiates, and those in California, Oregon, interior Washington and British Columbia and Idaho *C. b. hesperis*. Before this problem can be resolved, additional data are needed. Johnston's reports of voice pattern were subjective, i.e., did not include analysis of sonograms, and are equivocal. Additional morphological data are also needed, especially from birds with voice recordings. Also, if frequent mixed breeding by pairs having distinct calls of American and Northwestern crows (i.e., vocal type *C. b. hesperis* x vocal type *C. caurinus*) were documented, there would be evidence to support Johnston's (1961) recommendation for reclassification. Although Johnston's data strongly indicate a need for additional research, they do not warrant action by the A.O.U. committee at this time.

Townsend's Warbler (*Dendroica townsendi*)—Hermit Warbler (*D. occidentalis*)

The taxonomic category of superspecies is based on the assumption that adequate isolating mechanisms exist to prevent interbreeding should congeneric populations become sympatric. Consequently, as new information is obtained in zones of sympatry for superspecies, we should expect some systematic changes. Townsend's and Hermit warblers (along with *D. virens* and *D. chrysoparia*) are considered superspecies (A. O. U. 1983). Sympatric populations of *occidentalis* and *townsendi* occur in restricted areas of Oregon and Washington. Morrison and Handy (1983) have recently reported an analysis of *Occidentalis* x *townsendi* hybrids based on both phenotypic characteristics and song (via sonographic analysis). Their data indicate that hybridization has advanced beyond the first generation, i.e., several "backcrosses" were described. These data indicate a need for additional research that will disclose rates of hybridization and determine if assumed isolating mechanisms exist. Due to recognizable phenotypic characteristics, these data will be obtained more easily than for the previously described problem with crows.

Rosy Finch (*Leucosticte arctoa*)

The Gray-crowned Rosy Finch (*Leucosticte tephrocotis*), Black Rosy Finch (*L. artrata*), and Brown-capped Rosy Finch (*L. australis*) (A. O. U. 1957) are all now considered conspecific with the Asiatic Rosy Finch (*L. arctoa*). No literature is cited to support this sweeping merger of species (A.O.U. 1983), but recommendations by French (1969), Vaurie (1956, 1959), and Mayr and Short (1970) were probably considered. French (1959) provides limited evidence of intergrades between the Black and Gray-crowned Rosy finches, but these data are not sufficient to warrant a systematic change. Future research may prove this change to be correct, but the main point is that necessary data are not available to justify this action. Richard E. Johnson (pers. comm.) has studied rosy finches extensively for many years, and although his data are not completely analyzed, he also feels this change is premature. The systematic lumping of the rosy finches provides another extreme in interpretation by the Committee on Taxonomy and Nomenclature. We began this discussion with an example (i.e., Western Grebes) of no action despite much data that indicate the present classification is incorrect. In this last case, we see a fairly radical change with little supporting data from field research.

Acknowledgments

The writer thanks Leslie Ratti, Jay Rotella, and John Weber for reviewing the manuscript and providing helpful suggestions. Earl Godfrey kindly allowed reference to his unpublished data.

Literature Cited

American Ornithologists' Union. 1886. Check-list of North American Birds, 1st ed. Am. Ornithol. Union, New York.
———. 1895. Check-list of North American Birds, 2nd ed. Am. Ornithol. Union, New York.
———. 1931. Check-list of North American Birds, 4th ed. Am. Ornithol. Union, New York.
———. 1957. Check-list of North American Birds, 5th ed. Am. Ornithol. Union, New York.
———. 1973. Thirty-second supplement to the American Ornithologists' Union Check-list of North American birds. Auk 90:411-419.
———. 1983. Check-list of North American Birds, 6th ed. Am. Ornithol. Union, New York.

Arbib, R. 1983. Autumn book roundup: Check-list of North American birds. Am. Birds 37:835;919-921.
Baird, S. F. 1858. Birds. *In* Reports of explorations and surveys to ascertain the most practicable and economic route for a railroad from the Mississippi River to the Pacific Ocean, Vol. 9, part 2, Washington, D. C.
Coues, E. 1874. Check-list of North American birds. *In* Field Ornithology, Estes and Lauriat, Boston.
French, N. R. 1959. Distribution and migration of the Black Rosy Finch. Condor. 61:18-29.
Godfrey, W. E. 1966. The Birds of Canada. Natl. Mus. Canada Bull, No. 203, Biol. Ser, No. 73.
Hand, J. L. 1981. A comparison of vocalizations of western gulls (*Larus occidentalis* and *L. o. livens*). Condor 83:289-301.
Henshaw, H. W. 1881. On *Podiceps occidendalis* and *P. clarkii*. Bull. Nuttall Ornithol. Club 6:211-216.
Hoffman, W. J., J. A. Wiens, and J. M. Scott. 1978. Hybridization between gulls (*Larus glaucescens* and *L. occidentalis*) in the Pacific Northwest. Auk 95:441-458.
Johnson, N. K. 1980. Character variation and evolution of sibling species in the *Empidonax difficilis-florescens* complex (Aves:Tyrannidae). Univ. of Calif. Publications. Zoology, Vol. 112. Univ. of Calif. Press, Berkley.
Johnson, N. K. and R. M. Zink. 1983. Speciation in Sapsuckers (*Sphyrapicus*): I. Genetic differentiation. Auk 100:871-884.
Johnston, D. W. 1961. The Biosystematics of American Crows. Univ. of Washington Press, Seattle.
LeValley, R. R. 1980. The plumage sequence and taxonomy of the Yellow-footed Western Gull (*Laris occidentalis livens*). M.A. Thesis. Humboldt State University, Arcata, Calif.
Lowe, C. M. 1978. Certain life history aspects of the Red-tailed Hawk in central Oklahoma and interior Alaska. M.S. thesis, Univ. Alaska, Fairbanks.
Mayr, E. 1963. Animal species and evolution. Belknap Press of Harvard Univ. Press, Cambridge, Mass.
———. 1970. Populations, species and evolution. Belknap Press of Harvard Univ. Press, Cambridge, Mass.
——— and L. L. Short. 1970. Species taxa of North American birds. Nutall Ornithol. Club. Publ. No. 9.
Mindell, D. P. 1983. Harlan's hawk (*Buteo jamaicensis harlani*): a valid subspecies. Auk 100: 161-169.
Morrison, M. L. and J. W. Hardy. 1983. Hybridization between Hermit and Townsend's warblers. Murrelet 64:65-72.
Nuechterlein, G. L. 1981. Courtship behavior and reproductive isolation between Western Grebe color morphs. Auk 98:335-349.
Ratti, J. T. 1979. Reproductive separation and isolating mechanisms between sympatric dark- and light-phase Western Grebes. Auk 98:573-586.
———. 1980. The classification of avian species and subspecies. American Birds 34:860-866.
———. 1981. Identification and distribution of Clark's Grebe. Western Birds 12:41-46.
———. 1983. Morphological divergence between Western Grebe color morphs. J. Field. Ornithology 54:424-426.
Selander, R. K. 1971. Systematics and speciation. Pages 57-147 *in* D. S. Farner and J. R. King eds. Avian Biology, Vol. I. Academic Press, New York.
Smith, N. G. 1966. Evolution of some Arctic Gulls (*Larus*): An experimental study of isolating mechanisms. Ornithological Monographs No. 4.
Storer, R. W. 1965. The color phases of the Western Grebe. Living Bird 4:59-63.
Taverner, P. A. 1927. A study of *Buteo borealis*, the red-tailed hawk, and its varieties in Canada. Canada Dept. Mines, Victoria Mem. Mus., Mus. Bull No. 48, Biol. Series, No. 13.
Vaurie, C. 1956. Systematic notes on Palearctic birds. No. 20 Fringillidae: the genera *Leucosticte*, *Rhodopechys*, *Carpodacus*, *Pinicola*, *Loxia*, *Uragus*, *Urocynchramus*, and *Propyrrhula*. Am. Mus. Novitates No. 1786, Am. Mus. Nat. Hist., New York.
———. 1959. The birds of the palearctic fauna. A systematic reference: Order Passeriformes. H. F. & G. Witherby Limited, London.
Weber, J. W. 1981a. The *Larus* gulls of the Pacific Northwest's interior, with taxonomic comments on several forms (Part I). Continental Birdlife 2:1-9.
———. 1981b. The *Larus* gulls of the Pacific Northwest's interior, with taxanomic comments on several forms (Part II-conclusions). Continental Birdlife 2:74-91.

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian D. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1984 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaueuser Company, Centralia, Washington

1984 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Oregon Institute of Technology, Klamath Falls, Oregon
Oregon State University, Corvallis, Oregon
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
Saint Martin's College, Lacey, Washington
Seattle Central Community College, Seattle, Washington
Seattle Pacific University, Seattle, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State University, Pullman, Washington
Western Oregon State College, Monmouth, Oregon
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1984 Sustaining Individual Members

R. Michael Anthony, Bend, Oregon
Stephen F. Arno, Florence, Montana
Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
Robert L. Carr, Cheney, Washington
Tim W. Clark, Jackson, Wyoming
Richard G. Cline, Missoula, Montana
Susan G. Conrad, Corvalis, Oregon
George W. Douglas, Victoria, British Columbia, Canada
Arlene T. Doyle, Arcata, California
George R. Fahnestock, Seattle, Washington
William R. Funk, Pullman, Washington
Tom Gnojek, Soda Springs Idaho
Gerald H. Haddock, Wheaton, Illinois
Frederick C. Hall, Portland, Oregon
Charles R. Hatch, Moscow, Idaho
Francis R. Herman, Fairbanks, Alaska
Robert J. Jonas, Moscow, Idaho
Barry L. Keller, Pocatello, Idaho
John H. Larsen, Pullman, Washington
Denis P. Lavender, Corvallis, Oregon
Cal E. Meier, College Station, Texas
Emmett B. Moore, Jr., Richland, Washington
Howard R. Panik, Carson City, Nevada
William H. Rickard, Richland, Washington
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Ronald J. Taylor, Bellingham, Washington
Ralph L. Thompson, Berea, Kentucky
David D. Tillson, Salt Lake City, Utah
James M. Thorpe, Corvallis, Oregon
Daniel W. Uresk, Rapid City, South Dakota
Shepard M. Zedeker, Christiansburg, Virginia

Northwest Science

Information for Authors

The pages of *Northwest Science* are open to scientists in the basic, applied, and social sciences wherein original or fundamental research is presented. *Northwest Science* does not publish notes, letters, or bibliographic papers. Short papers are treated the same as longer manuscripts. All submissions are refereed, usually by two reviewers. Papers are also welcome from authors outside of the Pacific Northwest.

At least one of the authors of all papers considered for publication must be a member of the Northwest Scientific Association.

Manuscripts—Submit three copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten on 8½x11 paper and *double-spaced throughout (including abstract, acknowledgments, literature cited, tables, and legends for figures)*; provide ample margins. Computer printouts are not acceptable. Avoid unnecessary footnotes. Do not break words at the end of a line. Format and style of manuscripts should conform to general usage in recent issues.

An abstract, double-spaced and not exceeding five percent of the paper, should precede every article. The abstract should recapitulate the major points of the paper and should be suitable for use by abstracting services.

Literature citations should have the author's name and year of publication in the text; e.g. (Jones 1978). Citations should be double-spaced and listed in alphabetical order at the end of the article.

Present all data in international (SI) units. English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1982).

Equations should be presented camera-ready. Symbols should be large enough to be legible after a ⅓ to ½ reduction in size, but not overly large.

Tables should be typewritten (double-spaced) separately from the text. Original art work or glossy prints of photographs must be submitted for reproduction. Art work and lettering should be large enough (but not overly large) to provide clarity after a 50 percent reduction in size for printing. The author's name and figure number should be penciled on the back of each illustration. Provide a scale for distance on map illustrations. Legends for illustrations should be typed (double-spaced) as a section of the manuscript; do not use a separate page for each legend.

Length of manuscripts is limited to 15 pages of printed copy. Two typed pages are approximately equal to one journal page.

Authors of Biological Papers—On first mention, a species should be designated by common name followed by systematic binomial. For abbreviations and forms of titles for serial publications, follow the *BIOSIS List of Serials*. Consult with the *Council of Biology Editors (CBE) Style Manual*, 4th ed., for general information on manuscript preparation.

Correspondence—Correspondence should be between senior author and the Editor.

Editing—Manuscripts may be edited for grammatical correctness and clarity.

Galley Proofs and Reprints—One set of proofs will be sent to the senior author for correction shortly before publication; proofs should be returned to the Editor within three days of receipt. Senior authors should inform the Editor of any change of address for handling proofs. Reprints must be ordered when the proofs are returned. A schedule of reprint prices will be sent to the author with the proofs.

Page Charges—Page charges are currently $60 per printed page. Publication is not contingent upon payment of page charges, as the Association is prepared to assume them for members whose work is unsupported, but even partial payment would be helpful in order that we may continue this policy.

US ISSN 0029 344X

Northwest Science

Non-Profit Org.
BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

Quarterly Publication of the Northwest Scientific Association

Editor H. Clare Wiser Washington State University

Associate Editors

Botany	Robert L. Carr	Eastern Washington University
Chemistry and Physics	Frank L, Curzon	University of British Columbia
Engineering Mathemati	Carl L. Sheldon	Washington State University
Forestry		
Geology		
Social Scier		
Soils		
Zoology	Donald R. Johnson	University of Idaho

ALFRED R. HALVORSON
DEPT. OF AGRONOMY
WASHINGTON STATE UNIV.
PULLMAN WA
99164

Papers published in *Northwest Science* are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts,* and *University Microfilms.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.

Volume 58, Number 4

November 1984

Northwest Science

CONTENTS

243 A Comparison of Periphyton Growth on Artificial and Natural Substrates in the Upper Spokane River
Thomas S. Nielsen, William H. Funk, Harry L. Gibbons, and Robert M. Duffner

249 The Variation in Antagonistic **Streptomyces** Populations in Soils from Different Vegetation Types in Western Oregon
Anita Stiebrs Hutchins and Sharon L. Rose

256 A Method for Estimating Precipitation Amounts at Remote Field Sites
Robert R. Kindschy

262 Using Isozyme Analysis to Aid in Selecting Genetically Superior Ponderosa Pine for Coal-Mine Spoil Reclamation
Jack H. Woods, George M. Blake, and Fred W. Allendorf

269 Glaciation in the Lower Lewis River Basin, Southwestern Cascade Range, Washington
Maurice J. Mundorff

282 Demise of Spiny Hopsage Shrubs Following Summer Wildfire: An Authentic Record
W. H. Rickard and M. C. McShane

286 The Status of Wolverines in Colorado
David M. Nead, James C. Halfpenny, and Steve Bissell

290 Age-specific Productivity and Nest Site Characteristics of Cooper's Hawks **(Accipiter cooperii)**
Kevin R. Moore and Charles J. Henny

300 Daily Summer Movements, Activity Patterns, and Home Range of Pronghorn
Timothy D. Reynolds

312 The Susceptibility of Four Salmonid Species to the Eyefluke, **Diplostomum spathaceum**
Pollene Speed and Gilbert B. Pauley

317 Association News; Miscellaneous Announcements

Quarterly Publication of the Northwest Scientific Association

Northwest Scientific Association

(Founded 1923)

The Northwest Scientific Association, an affiliate of the American Association for the Advancement of Science, is an association representative of the basic and applied sciences and of social sciences.

Membership in the Northwest Scientific Association, which includes a subscription to *Northwest Science*, is open to individuals for $14 per year ($8 per year for students). Institutional memberships: (Washington, Idaho, Oregon, Western Montana, and British Columbia) less than 3000 students, $30; 3000 students or more $40. All other subscribers, $25 per year. Sustaining membership, $25 per year for individuals and $100 per year for organizations, institutions, or agencies. Subscriptions are for the calendar year only.

Send change of address, payment of dues, or requests for undelivered issues to the Treasurer.

Editor of *Northwest Science*
H. Clare Wiser
Department of Mathematics
Pullman, Washington 99164-2930
Washington State University

Officers of the Association

President Oscar Sziklai
University of British Columbia
Vancouver, B.C. (1985)*

Vice-President Ray A. Soltero
Eastern Wasington University
Cheney, Washington (1985)

Secretary Robert L. Carr
Eastern Washington University
Cheney, Washington (1984)

Treasurer Steven J. Brunsfeld
College of Forestry, Wildlife, and Range Sciences
University of Idaho
Moscow, Idaho 83843 (1986)

Past President Stephen F. Arno
USDA, Forest Service
Missoula, Montana (1985)

Trustees:

R. Alan Black
Washington State University
Pullman, Washington (1985)

T. A. (Andy) Black
University of British Columbia
Vancouver, British Columbia
(1985)

Lee E. Eddleman
Oregon State University
Corvallis, Oregon (1987)

William H. Emmingham
Oregon State University
Corvallis, Oregon (1987)

Donald Hanley
Washington State University
c/o University of Washington
Seattle, Washington (1986)

Susan Kephart
Willamette University
Salem, Oregon (1986)

Hubertus Kohn
Western Washington University
Bellingham, Washington (1987)

Thomas Nimlos
University of Montana
Missoula, Montana (1985)

M. A. Radwan
U.S. Forest Service
Olympia, Washington (1987)

Steven R. Seavey
Lewis and Clark College
Portland, Oregon (1985)

George G. Spomer
University of Idaho
Moscow, Idaho (1987)

Robert Stockhouse
Pacific University
Forest Grove, Oregon (1986)

B. J. Verts
Oregon State University
Corvallis, Oregon (1986)

*Term of office expires in the year given in parentheses.

PUBLISHED QUARTERLY (FEBRUARY, MAY, AUGUST, AND NOVEMBER) BY THE WASHINGTON STATE UNIVERSITY PRESS, PULLMAN, WASHINGTON 99164-5910

Thomas S. Nielsen[1]
William H. Funk
Harry L. Gibbons
Robert M. Duffner[2]
Department of Civil and Environmental Engineering
Washington State University
Pullman, Washington 99164-2912

A Comparison of Periphyton Growth on Artificial and Natural Substrates in the Upper Spokane River

Abstract

The purpose of the study was to determine preferences of periphyton for glass or natural substrates. Colonization of benthic samplers (baskets) was conducted in the Spokane River from December 1979 to November 1981. Standing crops of periphyton were estimated by ash-free dry weight, chlorophyll *a* density, and microscopic enumeration. Samples from rock substrate showed higher absolute values of chlorophyll *a* and ash-free dry weight (56 percent and 76 percent, respectively) than those collected from the glass substrate. Dominant periphytic genera were *Fragilaria* and *Synedra* of the Bacillariophyta, *Microspora* of the Chlorophyta, and *Lyngbya* of the Cyanophyta.

Introduction

The Spokane River originates at the mouth of Coeur d'Alene Lake and flows west to the Columbia River. This study encompassed an area along the course of the river in the eastern portion of the Spokane River valley (Fig. 1). Ten sampling stations were established along this reach of the upper Spokane River, from Harvard Road to the inflow of Hangman Creek. Each station was selected as representing some land-use aspect of the river. Harvard I and Harvard II stations were in areas used for animal grazing and farming. Barker, Sullivan, Euclid, Plantes Ferry, and Upriver stations represent portions of the river that run through the suburbs of the City of Spokane. The stations at Greene Street, Gonzaga University, and Hangman Creek are located within Spokane city limits.

The study was conducted between December 1979 and November 1981 as part of a larger investigation of the water quality of the Spokane River (Funk *et al.* 1983, Gibbons *et al.* 1984). Ranges of water quality conditions are shown in Table 1. Individual measurements are on computer file at the Environmental Engineering Section at Washington State University. Phytoplankton and macroinvertebrates also were intensively monitored during the investigation, and discussion of those communities can be found in Notestine (1982) and Duffner (1983).

Periphyton (attached algae) represent the algae of a river system. According to Round (1964), probably over 90 percent of all algae species grow in an attached form. Periphyton are also relatively fixed with regard to their position in a river and there-

[1]Present address: U.S. Army Environmental Hygiene Agency, Region South, Fort McPherson, Georgia 30330.

[2]Present address: City of Bellingham Public Works, 2221 Pacific Street, Bellingham, Washington 98226.

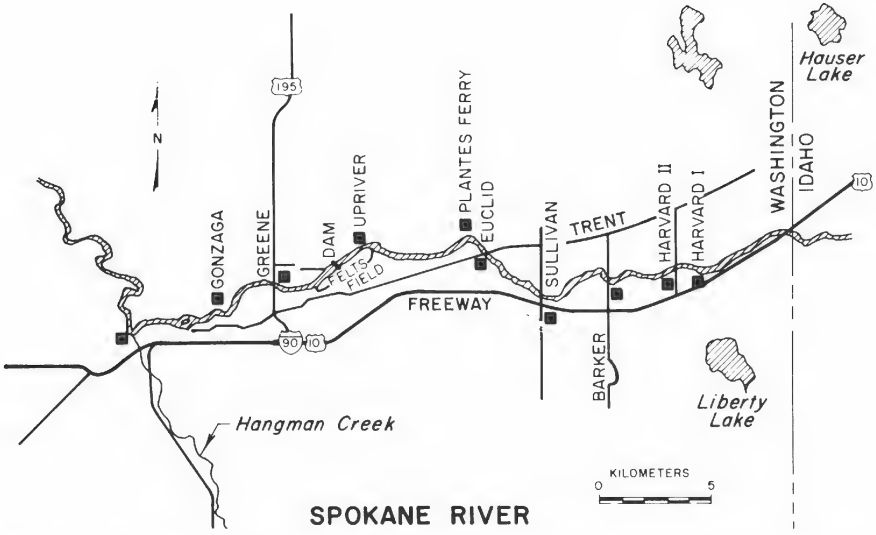

Figure 1. Upper Spokane River, from the Washington-Idaho stateline to Hangman Creek, with sites of sampling stations.

fore are more easily monitored than plankton, which are constantly being carried in and out of a study area by currents.

Periphyton are commonly regarded as indicators of water quality. They are valuable in these studies because they readily respond to changes in the aquatic environment. Chemical or physical measurements are useful parameters for describing water quality at a specific time, but an interpretation of the biomass and structure of a periphyton community exposed constantly to that water reflects the state of the environment on a long-term basis.

A number of studies have been conducted to compare periphyton growth on artificial (glass) and natural (rock) substrates. The conclusions regarding which substrate represents the better growing conditions for attached algae in a natural environment are

TABLE 1. Ranges of water quality parameters on the upper Spokane River, December 1979 to March 1981 (all values are mg/ℓ except as noted).

Parameter	Minimum	Maximum
Total Alkalinity (methyl orange alkalinity)	16.0	90.0
CO_2	0	3.0
Water Temperature (°C)	4.0	23.
Flow (C^3/S)	20.0	620.0
NO_2-N	0.01	0.01
NO_3-N	0.02	0.88
NH_3-N	0.01	0.01
Total Phosphorus	0.01	0.05
BOD	<1.0	4.8
Total Copper (µg/ℓ)	<1.0	8.0
Total Nickel (µg/ℓ)	<5.0	22.0
Total Cadmium (µg/ℓ)	<1.0	7.0
Total Lead (µg/ℓ)	<5.0	70.0
Total Zinc (µg/ℓ)	25.0	235.0

often conflicting. Siver (1977) and Tett *et al.* (1978) contended that glass slides are colonized by different species of periphyton, with different densities, than the natural substrates; hence, glass slides used for periphyton colonization do not reflect the composition of naturally occurring algal communities. Patrick *et al.* (1954) stated that glass slides collected a representative sample of the species of diatoms of a river, and McIntire (1966) found similar species of algae on glass and rock substrates. Wetzel (1975) believed that the number of discrepencies found between algal populations on natural and artificial substrata were sufficiently large to necessitate a thorough evaluation for each study.

The primary objective in studying the periphyton of the upper Spokane River was to determine if periphyton demonstrated a preference in colonizing rock or glass substrates. In addition, an assessment was made of the potential impact of the substrate on the ecological condition of the periphyton community by examining chlorophyll *a*, ash-free dry weight concentrations, and algae associations.

Methods and Materials

The responsiveness of periphyton to glass and rock substrates and to the water quality conditions of the Spokane River was measured by chlorophyll *a* analysis, ash-free dry weight and community structure by identification-enumeration. Substrates for the periphyton growth were provided by placing three glass rods and one or two flattened rocks into barbecue baskets that were set in the river at a depth of one meter. The glass rods were 8 cm in length with an outside diameter of 10 mm. A surface area of 25 cm^2 was provided. When the baskets were retrieved, the three glass rods were scraped and the periphyton rinsed into sampling bottles, one each to be analyzed for chlorophyll *a*, ash-free dry weight, and identification-enumeration.

The rocks in the baskets were gathered from the immediate vicinity of the site and were considered to be representative of rocks that periphyton would colonize. Rocks were chosen that were flat on one side and about 10 cm wide and up to 20 cm in length. A plexiglass ring with a neoprene seal was used to delineate an area of 11 cm^2 on the rocks. From these areas the periphyton were scraped, rinsed and siphoned as a slurry via a vacuum flask into three test tubes, to be analyzed in the same manner as the samples from the glass rods (Fig. 2).

The baskets were retrieved every 6 weeks during the warmer months (May to September) and every 12 weeks during the colder months (October to April). Such time periods are deemed sufficient to allow for the development of stable communities (American Public Health Association 1976).

Results and Discussion

The most common algal group sampled on either substrate was diatoms. The dominant diatom was the genus *Synedra*; it was found in concentrations as high as 21,000 cells/mm^2 in the winter months and was present during all seasons. The second most common periphytic form, *Fragilaria*, was found in densities of up to 16,000 cells/mm^2 in the late summer and winter, although it occurred throughout the entire year.

Other common diatoms encountered in the Spokane River were *Achnanthes, Amphora, Asterionella, Cymbella, Diatoma, Gomphonema, Melosira, Navicula*, and *Tabellaria.* All but *Asterionella* and *Melosira* are known to be stalked or to affix to the sub-

strate by various attachment mechanisms (Smith 1933; Prescott 1962, 1978; Patrick 1966). The presence of *Asterionella* and *Melosira*, plankton diatoms, among the attached algae can be attributed to the cells settling out on the substrate during periods of declining populations and quiescent water.

Diatoms often are grouped by genera into associations. Common associations include *Gomphonema-Diatoma* (Hynes 1970) and *Achnanthes-Gomphonema Synedra* (Round

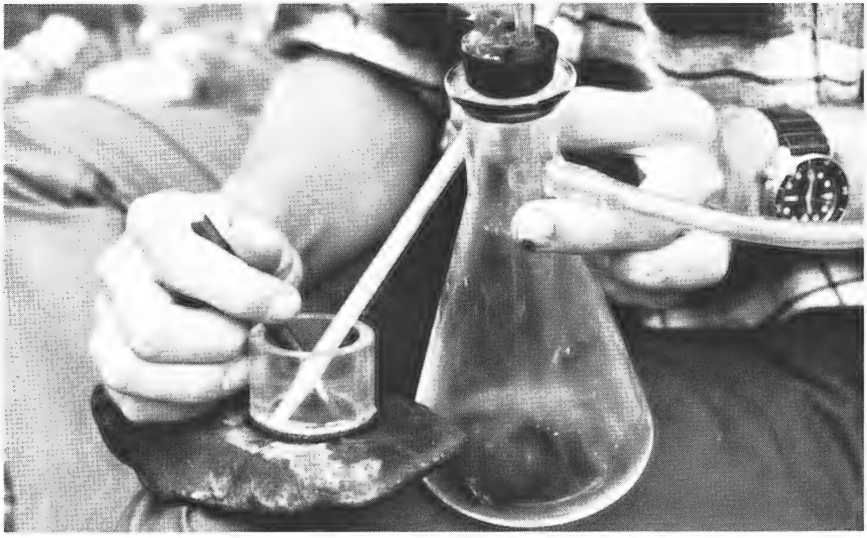

Figure 2. Aspirating device to remove periphyton from rock surfaces.

1965). The data presented in this study suggest that no associations exist between these genera in the Spokane River. This may be caused by the scouring of the river during high flow, the relatively high concentration of metals, or a combination of both factors.

Blue-green algae were the second most numerous group of algae encountered among the periphyton. The highest densities at all stations occurred during the summer months. On many occasions, *Lyngbya* was the only blue-green algae encountered, and when other blue-greens were present, *Lyngbya* made up the majority of cells.

Microspora was the most frequently encountered genus of the green algae found on the Spokane River. Other green algae observed included *Cladophora, Rhizoclonium* and *Ulothrix*.

According to Hynes (1970), green algae are expected to be a dominant periphyton group during the summer in a lotic environment. However, they were observed infrequently on the upper Spokane River. The high zinc concentrations encountered throughout the study period may have had an effect on the expected seasonal growth pattern of the Chlorophyta; further investigations are warranted. Earlier studies by Bartlett *et al.* (1974) showed complete inhibition of the test alga, *Selenastrum capricornutum*, by trace amounts of zinc.

Comparisons were made on the ash-free dry weight, chlorophyll *a* values, and the numbers of cells/cm^2 in the Bacillariophyta (diatom), Chlorophyta (green algae), and

Cyanophyta (blue-green) algae groups to determine if a preference was demonstrated for rocks or glass substrate. In addition, paired t-test (Huntsberger and Billingsley 1977) were conducted; the null hypothesis was that no selectivity for rocks or glass substrate was observed at the 95 percent confidence level except that to be expected by chance (Table 2). All data were normalized by base 10 logarithms (Bliss 1967).

TABLE 2. Summary of paired t-test for substrate preference.

Parameter Tested	Mean Difference	Variance	n	Calculated t	Table t	Reject Null Hypothesis
Ash-free dry weight	3.56 mg/cm^2	2.07	62	5.42	2.00	Yes
Chlorophyll[a]	0.48 µg/cm^2	1.39	65	2.13	2.00	Yes
Diatoms	-0.196 cells	2.22	55	-0.96	2.01	No
Green algae	-206 cells	10.55	48	-0.92	2.01	No
Blue-green algae	-918 cells	12.31	49	1.29	2.01	No

The densities of algae cells were higher on the rock substrate than on the glass substrate in 51 percent of the Cyanophyta samples, in 45 percent of the Bacillariophyta samples, and in 41 percent of the Chlorophyta samples. The paired t-test indicated that no significant difference was demonstrated in the numbers of cells of the major algae groups colonizing the rock or glass substrate. The rock substrate was observed to have higher chlorophyll *a* and ash-free dry weight concentrations than the glass substrate in 56 percent and 76 percent of the samples, respectively. The null hypothesis of the paired t-test was rejected for chlorophyll *a* and ash-free dry weight. These results indicate that periphyton colonized the substrates in a random fashion, but once established, they were better able to carry on primary production on the rock substrate than on the glass, as demonstrated by the higher ash-free dry weight and chlorophyll *a* values. The significantly greater amounts of ash-free dry weight and chlorophyll *a* on the rock substrate seems to indicate that the rougher rock substrate provides a more productive habitat for the algae. Periphyton can attach more easily to the rough rock than to the smooth glass, and interstices in the rock provide better havens from the scouring action of the current than the smooth glass. Horner and Welch (1981) found that growth increased with increased current until the velocity caused a severe shearing of the periphyton.

The periphyton measurements reinforce the results of earlier studies on the effect of flow on algal production. A dam creates a lentic situation at the Upriver station; at the other nine stations the river is characterized by a moderate to swift flow. At the Upriver station the rock substrate had more ash-free dry weight than the glass substrate on 61 percent of the samples; the chlorophyll *a* values were greater on the rock substrate in only 42 percent of the samples. At all other stations the rock substrate had higher ash-free dry weight and chlorophyll *a* concentrations than the glass substrate in 78 percent and 58 percent of the samples, respectively. That is, at a station where flow was not as great, there was less difference in periphyton production on rock versus glass substrates.

Summary

The study, conducted on the upper Spokane River to determine algae selectivity for artificial or natural substrate, indicated that the periphyton showed no definable difference in density between the algae colonizing glass and natural rock substrate. How-

ever, once the periphyton were attached to the rock substrate, they were able to attain a greater ash-free dry weight and chlorophyll *a* level than the same density of algae on the glass substrate. Hence, the periphyton on the rock substrate had an advantage over the periphyton on the glass substrate in the process of primary production. It appears that consideration of artificial substrate composed of glass would lead to underestimation of periphyton productivity in flowing waters.

Acknowledgments

This investigation was made possible by a grant from the Washington State Department of Ecology, DOE Project Number WF 80-002. The authors thank Gary Bailey and Paul Bennett for technical aid, and the staff of the State of Washington Water Research Center for critical review and manuscript preparation.

Literature Cited

American Public Health Association. 1976. Standard Methods for the Examination of Water and Wastewater. 15th ed.

Bartlett, L. D., F. W. Rabe, and W. H. Funk. 1974. The effect of copper, zinc, and cadmium on *Selenastrum capricornutum*. Water Res. 8:179-185.

Bliss, C. J. 1967. Statistics in Biology. McGraw-Hill.

Duffner, R. M. 1983. Investigation into Sampling Methods for Benthic Macroinvertebrates in a Large Fast Flowing River. M.S. Thesis, Wash. State Univ., Pullman, Washington.

Funk, W. H., H. L. Gibbons, R. M. Duffner, T. Notestine, and T. Nielsen. 1983. Water Quality of the Upper Spokane River and Evaluation of Methods for Measurement of the Effect of Effluent Upon Primary and Secondary Producers. State of Washington Water Research Center Report 48, Pullman, Washington.

Gibbons, H. L., Jr., W. H. Funk, R. M. Duffner, T. S. Nielsen, and T. Notestine. 1984. Baseline Study to Determine the Water Quality and the Primary and Secondary Producers of the Spokane River, Phase I. Project completion report to the State of Washington Department of Ecology (Project No. WF 80-002). State of Washington Water Research Center Report 57, Pullman, Washington.

Horner, R. R., and E. B. Welch. 1981. Stream periphyton development in relation to current velocity and nutrients. Can. J. Fish. Aquat. Sci. 38:449-457.

Huntsberger, D. V., and P. Billingsley. 1977. Elements of Statistical Inference. Allyn and Bacon.

Hynes, H. B. N. 1970. The Ecology of Running Waters. Univ. Toronto.

McIntire, C. D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiologia. 27:559-570.

Notestine, T. H. 1982. A Comparison of Attached Algal Communities on Natural and Artificial Substrates in the Upper Spokane River. M.S. Thesis, Wash. State Univ., Pullman, Washington.

Patrick, R., M. H. Hohn, and J. H. Wallace. 1954. A new method for determining the pattern of diatom flora. Notulae Naturae of Acad. of Nat. Sci. of Philadelphia. 259:1-9.

———, and C. W. Reimer. 1966. The Diatoms of the United States. Acad. of Natl. Sci. of Philadelphia.

Prescott, G. W. (ed.). 1962. Algae of the Western Great Lakes Area. Wm. C. Brown.

——— (ed.). 1978. How to Know the Freshwater Algae. Wm. C. Brown. Round, F. E. (ed.). 1964. The ecology of benthic algae. *In* Jackson, D. F. Algae and Man. Plenum Press.

——— (ed.). 1965. The Biology of the Algae. Edward Arnold Ltd. Siver, P. A. 1977. Comparison of attached diatom communities on natural and artificial substrates. J. Phycol. 13:402-406.

Smith, G. M. (ed.). 1933. The Freshwater Algae of the United States. McGraw-Hill.

Tett, P., C. Gallegos, M. G. Kelly, G. M. Hornberger, and B. J. Cosby. 1978. Relationships among substrate, flow, and benthic microalgal pigment density in the Mechums River, Virginia. Limnol. Oceanogr. 23:785-797.

Wetzel, R. G. 1975. Limnology. W. B. Saunders.

Received, February 7, 1983
Accepted for publication, April 4, 1984

Anita Stiebrs Hutchins

Forestry Sciences Laboratory
Pacific Northwest Forest and Range Experiment Station
Corvalis, Oregon 97331

and

Sharon L. Rose

Department of Forest Science
School of Forestry
Oregon State University
Corvallis, Oregon 97331

The Variation in Antagonistic Streptomyces Populations in Soils from Different Vegetation Types in Western Oregon

Abstract

Grassland, red alder, and Douglas-fir soils were examined for total number of microorganisms recovered from dilution plating, the number of *Streptomyces*, and the percentage of *Streptomyces* isolates antagonistic to the test fungus *Phellinus weirrii* (Murr.) Gilb. The Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) site with no apparent or obvious *P. weirii* activity had the highest percentage of antagonistic *Streptomyces*. Plant communities had distinctively different populations of antagonistic *Streptomyces* species and communities with the greatest diversity of vascular plant species supported the greatest diversity of antagonistic *Streptomyces* species.

Introduction

Investigators have shown that both the number and species composition of soil microbes reflect the species diversity and composition of vascular plant communities (Kuster 1976, Wicklow *et al.* 1974). Wicklow *et al.* (1974) found more fungal species in forest soil with a diverse tree community than in a more homogeneous forest. The number and antibiotic activity of *Streptomyces* species are also thought to be influenced by the composition of vascular plant communities. Abraham and Herr (1964) suggested that every plant species fosters a particular *Streptomyces* flora. Both the number of individual *Streptomyces* species and species diversity of the *Streptomyces* population are generally considered to be higher in grassland soils and pastures than in forested sites (Alexander 1977). Hutchins and Li (1981) reported that soils under conifer and alder were strikingly different in the number and species of *Streptomyces* antagonistic to *Phellinus weirii* (Murr.) Gilb., a pathogenic fungus inducing a serious root rot of conifers in Western North American forests. Rangaswami and Ethiraj (1962) found that three primary factors influenced *Streptomyces* antibiotic production in soil: (1) number and composition of the microbial population, (2) soil pH, and (3) the organic matter content.

In this study we examined the *Streptomyces* species we recovered by dilution-plate techniques on selective media from soil samples from six plant communities in western Oregon to determine if populations were different and whether any such differences were correlated with the type of vascular plant cover. We also compared the percentage

of soil *Streptomyces* antagonistic to *P. weirii* in grassland, alder and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest soils to determine if the presence of a coniferous host of *P. weirii* influenced the species composition and number of native *Streptomyces* antagonistic towards this fungal pathogen. Antagonistic *Streptomyces* colonies were isolated and identified as to species in an attempt to qualify and quantify differences in the species composition of *Streptomyces* antagonistic to *P. weirii*.

Methods and Materials

Six areas in western Oregon were selected representing three vegetative communities: grasslands, red alder (*Alnus rubra* Bong.), and Douglas-fir.

One grassland site at 62 m elevation was part of a 100-year-old cemetery 10 miles south of Corvallis, Oregon, in the Willamette Valley, on a Woodburn-Willamette silt loam soil. The vegetative community is composed primarily of four grass species: *Festuca rubra* L., *Agropyron repens* (L.) Beauv., *Lolium perenne* L., and *Sorghum halepense* (L.) Pers. This site has been in grassland vegetation for over 100 years and is surrounded by oak and a Douglas-fir forest.

The other grassland site was a natural meadow at 1249 m elevation on Mary's Peak in the Oregon Coast Range on an Apt-Honeygrove-Bohannon association of silty clay loam soils. The vegetation is predominantly red fescue (*Festuca rubra* L.) and sedge (*Carex californica* Bail.). The forest adjacent to the meadow is comprised of Douglas-fir and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.).

Red alder is an aggressive pioneer species in the coastal regions and two red alder communities were chosen for sampling. One was a 40-year-old stand growing on a gravelly clay loam at 199 m in the Oregon Coast Range with an understory of vine maple (*Acer circinatum* Pursh), thimbleberry (*R. parviflorus* Nutt.), salmon-berry (*Rubus spectabilis* Pursh), western sword fern (*Polystichum munitum* Kaulf.) Presl), and various cryptogams. A Douglas-fir forest surrounds this alder site. The other alder stand was from a sand dune community 8 km north of Waldport on the Oregon coast. Individual alder trees with associated grass species were growing on stable dunes. The vegetation changes abruptly to shore pine (*Pinus contorta* Dougl. ex Loud.) a short distance from the alder stand.

A 50-year-old Douglas-fir stand at 100 m elevation on a Slickrock gravelly clay loam soil was sampled in the Oregon Coast Range, 10 miles west of Corvallis, Oregon. We chose two sites from this stand. In one, *Phellinus weirii* was causing windthrow and mortality in a large portion of the stand while in the second site there did not appear to be any *P. weirii* activity and no tree mortality. The understories in both sites consisted mainly of long-leaved Oregon grape (*Berberis nervosa* Pursh), western sword fern, wood sorrel (*Oxalis trilliifolia* Hook), and various cryptogams. About 5 cm of litter, mostly Douglas-fir needles and twigs, covered the soil.

Each site was sampled at three locations (plots) in November and May. We ran a transect across each location and collected a soil subsample using a 2 cm soil auger from 12 positions spaced at 5 m intervals across the transect at each of the three plots. The twelve samples, from the surface of mineral soil to 25 cm depth, were combined and mixed to give a composite sample of about 1000 g soil/plot. The soil was sifted through a 2 mm screen and the moisture content was determined by drying at 60° C until a constant weight was reached. Soil was analyzed by the Soil Testing Laboratory,

Oregon State University (Table 1). Organic matter was determined by the Walkley-Black method (Alexander 1977); nitrogen by Kjeldahl Method (Isizawa and Araragi 1976); extractable K, Mg, and Ca were determined by atomic absorption spectrophotometric techniques; available phosphorus was determined by the sodium bicarbonate extraction technique (Watanabe and Olsen 1965); soil reaction (pH) was measured from a water saturation paste on a pH meter.

Soil dilutions using 20 gm/soil plot at the following dilutions 1/100, 1/1000, 1/10,000 were prepared and 3 replications of 1 ml of each dilution were plated on sodium albuminate agar (pH 6.8), a selective medium for *Streptomyces* and non-filamentous or true bacteria (Johnson *et al.* 1965). Colonies were counted after incubation at 28° C for eight days. Colonies of true bacteria and *Streptomyces* were counted under asceptic conditions and colonies of *Streptomyces* isolated onto selective media. Individual colonies of true bacteria were distinguishable from *Streptomyces* by colony characteristics as observed under 10 and 100 × magnification. Hyphal tips from individual *Streptomyces* colonies were transferred to tubes containing sodium albuminate agar, and incubated for two weeks at 28° C. Each *Streptomyces* isolate growing in pure culture was assessed for antagonism against *P. weirii* by using the cross-inoculation assay method of Johnson and Carl (1972). *Streptomyces* isolates in pure culture were transferred to a buffered malt-yeast-peptone agar plate (Hutchins 1980) opposite a culture of *P. weirii.* The buffered malt-yeast-peptone (B-MYP) medium facilitated good growth of both *Streptomyces* and *P. weirii* while the pH remained unchanged. Plates were incubated at 26° C in the dark for two weeks and inspected for a clear zone around the *Streptomyces* colony, indicative of antibiosis. Approximately 250 *Streptomyces* colonies isolated from each site in May, and again in November, were tested for antagonism to *P. weirii.*

The dominant antagonistic *Streptomyces* colonies isolated were identified to species by methods described by Shirling (1968), Shirling and Gottlieb (1966, 1968, and 1969), and modified by Kuster (1976). Color of the aerial mycelium and of the reverse, color of soluble pigment, melanin production, and the morphology of sporophores and spores were noted on pure cultures of the isolated *Streptomyces.* Carbohydrate utilization and growth rates were determined with sucrose, D-mannitol, L-arabinose, D-xylose, D-fructose, rhamnose, i-inositol, and raffinose. Glucose added to B-MYP medium was used as the positive control and B-MYP media without carbohydrate as a negative control. Electron micrographs were used to determine sporophore and spore morphology.

TABLE 1. Chemical analyses of soils sampled.

	Determinations								
Site	pH	P (ppm)	K (ppm)	Ca (meq/100g)	Mg (meq/100g)	CEC[1]	% C	% N	C/N
Grass cemetery	6.1	44	468	10.2	3.1	20.64	3.24	.212	15.2
Grass meadow	5.0	27	343	1.5	0.8	45.24	11.80	.924	12.8
Alder forest	5.0	14	636	22.3	8.3	46.90	5.40	.304	17.8
Alder sand	5.9	11	62	0.3	0.2	0.86	0.11	.004	27.5
Conifer (**P. weirii** uninfested)	5.8	60	390	7.2	2.4	26.06	4.61	.205	22.5
Conifer (**P. weirii** infested)	5.6	46	421	10.7	3.6	40.48	7.15	.300	23.8

Differences among total bacterial numbers, number of *Streptomyces* isolates, and percentages of antagonistic *Streptomyces* at each of the six sites were tested for statistical significance by one-way analysis of variance (ANOVA).

Results and Discussion

We found the least diverse populations of antagonistic *Streptomyces* on sites with the least diverse vascular plant communities (Table 2). The antagonistic *Streptomyces* isolates from the grass cemetery site were dominated by one species which accounted for 96 percent of the isolated *Streptomyces*. The *Streptomyces* colonies isolated from the grass meadow site were dominated by one species which accounted for 71 percent of the total isolates. In the sites with more vascular plant diversity and heterogeneiety, the alder forest and the two conifer stands, the antagonistic *Streptomyces* were composed of many co-dominant species. These results parallel those of Wicklow *et al.* (1974), who reported an increase in the number of fungal species in forest stands that had a comparatively higher number of vascular plant species.

Several authors have suggested that similar vegetative communities would have similar microbial populations (Alexander 1977, Kuster 1976, Weste and Vithanage 1978). *Streptomyces atroolivaceus*, the dominant species in the alder sand dune site, and *S. gelaticus*, a co-dominant species from the alder forest site, have previously been reported from alder soils (Hutchins and Li 1981). Also, *S. longisporus* and *S. parvulus*, the dominant and co-dominant species from the conifer site, with *P. weirii* mortality have been isolated from conifer rhizohpheres (Hutchins and Li 1981, Knutson *et al.*

[1]Cation exchange capacity.

TABLE 2. Antagonistic **Streptomyces** populations isolated from six communities in November.

Site	Total number of antagonistic **Streptomyces** species per site	**Streptomyces** species isolated	**Streptomyces** Percent of total number
Grassland cemetery	72	**S. lydicus** DeBoer, Dietz, Silver and Savage	96
Grassland meadow	28	**S. longisporus** Krasilnikov	71
		S. aerocolonigenes Shinobu and Kawato	7
		S. griseoruber Yamaguchi and Saburi	7
Alder forest	19	**S. orientalis** Pittenger and Brigham	21
		S. filipinensis Ammann, Gottlieb, Brock, Carter, and Whitfield	21
		S. gelaticus (Waksman) Waksman and Henrici	16
Alder sand	21	**S. atroolivaceus** Preobraszhenskaya, Blinov, and Ryabova	38
		S. albofaciens Thirumalacher and Bhatt	24
		S. pseudogriseolus Okami and Umezawa	10
Conifer (**P. weirii** uninfested)	57	**S. longisporus** Krasilnikov	40
		S. sp. 90	11
		S. parvulus Waksman and Gregory	7
		S. fasciculatus Pittenger and Nelms	5
		S. sp. 98	4
		S. sp. 133	4
		S. sp. 135	4
Conifer (**P. weirii** infested)	28	**S. sioyaensis** Nishimura, Okamota, Mayama, Ohtsuka, Nakajima, Tawara, Shimohira, Shimaoka	10
		S. albiflavus Waksman and Henrici	7
		S. violescens Preobrazhenskaya and Sueshnikova	7
		S. albus (Rossi-Doria) Waksman and Henrici	7
		S. chibaensis Suzuki, Nakamura, Okuma, and Iomiyama	7
		S. sp. 147	

1980). *Streptomyces longisporus*, however, was also isolated from the grass meadow site, suggesting that some species of *Streptomyces* have a less host-vegetation-specific distribution. Our finding of little species overlap between communities suggests that a specific and definable microbial community related to dominant vascular plant vegetation may exist in each habitat.

Soil factors also influence the soil microbial community. Soils high in humus and rich in nitrogenous materials are reported to have more non-antibiotic-producing *Streptomyces* than antibiotic-producing *Streptomyces* (Isizawa and Araragi 1976, McGahen 1951, Thaysen 1950). This was also true in our study; the *P. weirii* infested conifer soil with higher levels of C and N had a low percentage of antagonistic *Streptomyces*, while the soil from the conifer site without *P. weirii* activity, with lower C and N, had a high percentage of antagonists (Tables 1 and 2). The grass meadow site, however, with the highest C and N content, and a C/N ratio of 12.8, had an intermediate percentage of antagonistic *Streptomyces* species. Whether high levels of nitrogen influence the number of antibiotic producing *Streptomyces* is problematic at best since increasing levels of nitrogen have not slowed the spread of *Phellinus weirii* in soil (Wallis and Reynolds 1974). In addition, antibiosis could be influenced by other soil characteristics or to aspects of general soil microbial populations.

Fifty-seven antagonistic *Streptomyces* isolates were recovered from soil taken from the uninfested Douglas-fir stand where no *P. weirii* activity was evident. In the *P. weirii* infested site, only 28 antagonistic *Streptomyces* isolates were recovered. These results suggest a possible relationship between a more species diverse antibiotic *Streptomyces* populations and the absence of the pathogen. Weste and Vithanage (1978) reported that *Phytophthora cinnamomi* Rands, a true soil borne pathogen, is most abundant where competitive microorganisms are few. A reduction in actinomycetes in the diseased rhizosphere probably means a reduction in antibiosis (Weste and Vinghange 1978). Our results suggest possible suppression of *P. weirii* in the soils by endigenous *Streptomyces* species.

The highest number of total bacterial was found in the grass cemetery and grassland meadow sites (Table 3). The alder sand dune site, on the most nutritionally deficient soil, supported the lowest population of true bacteria and *Streptomyces*. Although there was no significant difference between the numbers of total bacteria at the two

TABLE 3. Microbial populations and percentages of **Streptomyces** isolates antagonistic to **P. weirii** from soil sampled during November and May from six vegetative communities in western Oregon.

Site	Mean Total Bacterial Counts[1]		Means **Streptomyces** Counts[1]		% Antagonistic **Streptomyces**	
	November	May	November	May	November	May
Grass cemetery	13.87^{a+}	11.84^{a}	9.16^{a}	6.68^{a}	28^{a}	34^{a}
Grass meadow	7.59^{b}	11.42^{a}	2.93^{b}	5.30^{a}	29^{a}	46^{a}
Alder forest	8.34^{b}	13.66^{a}	5.81^{c}	6.10^{a}	12^{a}	10^{b}
Alder sand dune	0.20^{c}	0.15^{b}	0.05^{d}	0.06^{b}	21^{a}	14^{b}
Conifer (**P. weirii** uninfested)	2.19^{c}	9.63^{a}	$1.28^{b,c}$	6.52^{a}	67^{b}	49^{a}
Conifer (**P. weirii** infested)	2.07^{c}	8.73^{a}	0.62^{e}	5.26^{a}	31^{a}	17^{b}

[1]Colonies x 10^{6} per gram of soil.

+a-e: Numbers with the same superscript are not significantly different at the P = .01 level.

conifer sites, there was a significantly lower number of *Streptomyces* colonies in the soil from the *P. weirii* infested stand than in soil samples from the apparently uninfested stand (Table 3).

The areas we sampled are fundamentally different from one another and we were able to observe significantly different levels of antagonism against *P. weirii* among our sites. Assuming that antagonism against *P. weirii* is an indirect measure of the incidence of a general antibiotic-producing *Streptomyces* population, we suggest that the population of antibiotic-producing *Streptomyces* responds to the vascular plant community in general, and to the presence of a potential pathogen and host in particular. However, our work, limited to sites and soils of western Oregon, should not be extrapolated to other regions and to other plant communities. The determination of the absolute presence or absence of *P. weirii* from a site is a prerequisite for future studies on suppression of *P. weirii* by the soil microflora. The development of *P. weirii* selective medium will enable us to assay the soil for this organism. When developed, more intensive sampling in infested vs. uninfested stands in this and in other regions must be done to determine whether the differences in *Streptomyces* populations and the percent antagonism are related to the presence and behavior of *P. weirrii*, and whether this phenomenon is general and widespread.

Acknowlegments

The technical assistance of Mr. Harlan Fay is greatly appreciated.

Literature Cited

Abraham, T. A., and J. Herr. 1964. Activity of actinomycetes from rhizohphere and non-rhizosphere soils of corn and soy bean in flour physiological tests. Can. J. Micro. 10:281-285.

Alexander, M. 1977. Introduction to Soil Microbiology. John Wiley and Sons, New York.

Black, C. A. (ed.). 1965. Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. Am. Soc. Agron., Madison, Wis.

Hutchins, A. S. 1980. In vitro inhibition of root-rot pathogens *Phellinus weirii*, *Armillariella mellea*, *Fomes annosus*, and *Phytophthora cinnamomi* by a newly isolated *Bacillus* sp. Micro. Ecology 6:253-259.

Hutchins, A. S., and C. Y. Li. 1981. Relative capacities of filamentous and non-filamentous bacteria from two forest soils to inhibit *Phellinus weirii* in culture. Northw. Sci. 55:219-224.

Isizawa, S., and M. Araragi. 1976. Composition of actinomycete populations in soil. Pp. 97-107. *In* T. Arai (ed.), Actinomycetes, The Boundary Microorganisms. Toppan Co. Ltd., Tokyo.

Jackson, M. L. 1958. Soil Chemical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Johnson, L. F., and E. A. Curl. 1972 Methods for Research on the Ecology of Soil Borne Plant Pathogens. Burgess Publishing Co., Minneapolis.

Johnson, L. F., E. A. Curl, J. H. Bond, and H. A. Fribourg. 1965. Methods for Studying Soil Microflora-Plant Disease Relationships. Burgess Publishing Co., Minneapolis.

Knutson, D. M., A. S. Hutchins, and K. Cromack. 1980. Isolation and identification of calcium-utilizing *Streptomyces* from conifer ectomycorrhizae and other rhizosphere sites. Antonie van Leeuwenhock 46:611-619.

Kuster, E. 1976. Simple working key for the classification and identification of named taxa included in the International *Streptomyces* Project. Int. J. of Systematic Bacteriol. 22(3):139-148.

———. 1976. Ecology and predominance of soil streptomycetes. Pp. 109-121. *In* T. Arai (ed.), Actinomycetes, The Boundary Microorganisms. Toppan Co. Ltd., Tokyo.

McGahen, J. W. 1951. Soil amendments in relation to the Actinomycete population and the antibiotic index of sugar-cane soil. Phytopathology 41:25.

Rangaswami, G., and S. Ethiraj. 1962. Antibiotic production by *Streptomyces* spp. in unamended soil. Phytopathology. 31:989-992.

Shirling, E. B. 1968. Cooperative description of type cultures of *Streptomyces*. II. Species descriptions from first study. Int. J. Systematic Bacteriol. 18(2):29-189.

Shirling, E. B., and D. Gottlieb. 1966. Method for characterization of *Streptomyces* species. Int. J. of Systematic Bacteriol. 16(3):313-340.

Shirling, E. B., and D. E. Gottlieb. 1968. Cooperative description of type cultures of *Streptomyces*.

III. Additional species descriptions from first and second studies. Int. J. Systematic Bacteriol. 18:279-392.
———, and ———. 1969. Cooperative descriptions of type cultures of *Streptomyces*. IV. Species descriptions from the second, third, and fourth studies. Int. J. Systematic Bacteriol. 19:391-512.
Thaysen, A. C. 1950. Antibiotics in the soil. Nature 166:93-94.
Wallis, G. W., and G. Reynolds. 1974. Urea and nitrate fertilizers fail to inhibit root rot. Bimonthly Research. Notes Forest Service, Canada. 30:25-26.
Watanabe, F. S., and S. R. Olsen. 1965. Test of an ascorbic acid method for determining phosphorus in water and $NaHCO_3$ extracts from soil. Soil Sci. Soc. Am. Proc. 26:677-678.
Weste, G., and K. Vithanage. 1978. Effect of *Phytophthora cinnamomi* in microbial populations associated with the roots of forest flora. Aust. J. Microbiol. 26:153-167.
Wicklow, M. C., W. B. Bollen, and W. C. Denison. 1974. Comparison of soil microfungi in 40-year-old stands of pure alder, pure conifer, and alder-conifer mixtures. Soil Biol. Biochem. 6:73-78.

Received March 25, 1983
Accepted for publication, Oct. 18, 1983

Robert R. Kindschy
USDI Bureau of Land Management
P. O. Box 700
Vale, Oregon 97918

A Method for Estimating Precipitation Amounts at Remote Field Sites

Abstract

Analysis of precipitation amounts occurring on the arid sagebrush steppe of southeastern Oregon revealed significant correlation with elevation ($P < .01$). Analysis of data provided an equation for predicting precipitation at remote field sites. Predictions were subsequently compared with actual measurements at 15 newly establshed precipitation gauges. Regression analysis proved predictions to be significant, to highly significant, among the years. Precipitation estimates may be used to forecast vegetative response during the subsequent growing season.

Introduction

Production of vegetation on comparable sites within the semiarid rangelands of the intermountain western United States is more influenced by precipitation occurring during the Crop Year (September through June inclusive) than by any other variable. Precipitation amount increases with elevation in most instances (Helvey and Fowler 1982). Knowledge of pending vegetative growth is important for land management decisions regarding livestock and wildlife forage production, and for fuel loads for fire hazard predictions.

The sparse distribution of weather stations typical of the intermountain rangeland area does not allow site specific analysis of localized precipitation. Rangeland managers need to adjust livestock grazing intensity within fenced pastures. Similarly, big game habitat managers require information on potential browse shrub production to determine adequate harvest levels, thus reducing the likelihood of massive winter game mortality. Site specific precipitation information is generally lacking for analysis of vegetative production within localized areas.

Study Area

Southeastern Oregon is here defined as the northern half of Malheur County, an area of approximately 13,800 km^2 (Fig. 1(. Topography varies from rolling to mountainous. Elevations range from 670 m near the Snake River to 2,381 m at the summit of Ironside Mountain. The mean crop year (CY) precipitation for seven National Oceanic and Atmospheric Administration (NOAA) stations during the 17 year period of 1966 through 1982 was 26.43 cm (SD = 3.49). Station elevation averaged 1,045 m with a range of 683 m to 1,408 m (Table 1).[1]

[1]Climatological Data. E.P.S., N.O.A.A., U.S. Department of Commerce.

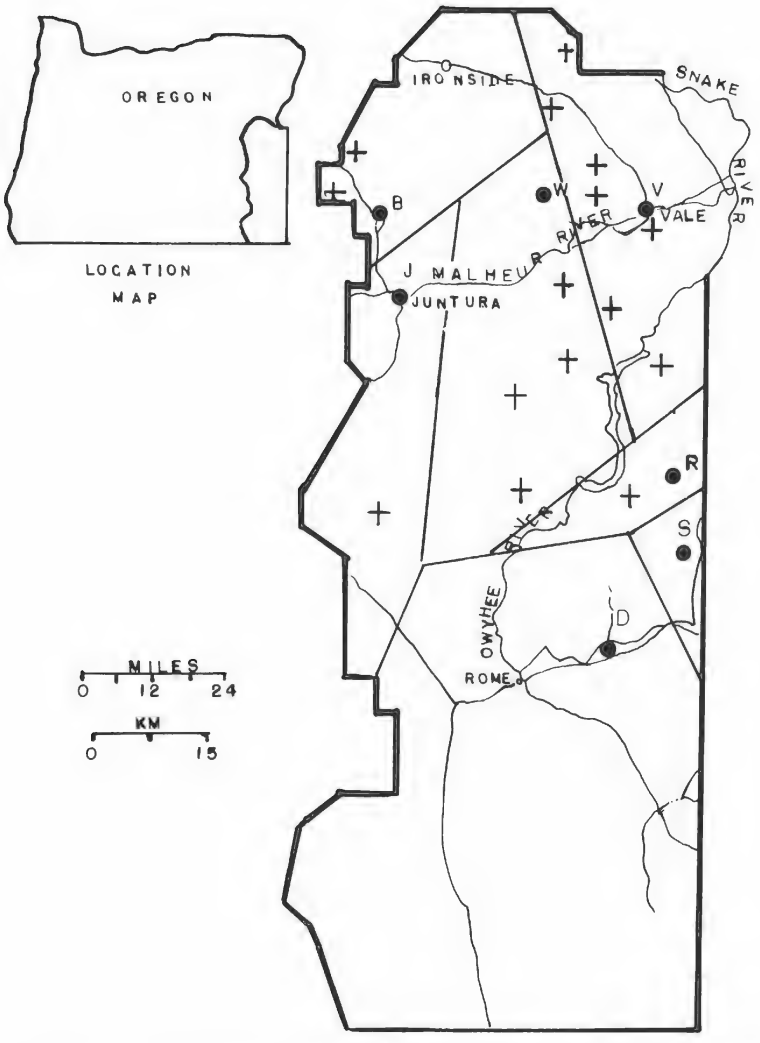

Figure 1. Study area in southeastern Oregon. ● = NOAA stations, + = BLM remote gauges, ⋈ = NOAA station polygon.

TABLE 1. Elevations and 17 year arithmetic mean CY precipitation of 7 NOAA weather stations within northern Malheur County, Oregon.

NOAA Station	Elevation (m)	Mean CY Precipitation (cm)
Beulah	997	24.7
Danner	1,288	27.4
Juntura	863	22.7
Rockville	1,119	25.5
Sheaville	1,408	29.0
Vale	683	21.1
Westfall	957	21.2

Previous Work

A positive correlation between increases in elevation and increased precipitation in middle and high latitudes has been recognized (Henry 1919, Lull and Ellison 1950). Helvey and Fowler (1982) described the variation in annual precipitation in the Columbia Basin of Washington. Sneva and Calvin (1978) developed an improved Thiessen polygon grid for eastern Oregon utilizing data from long term weather stations. Although past workers have documented that correlation coefficients between stations decreased as horizontal distance between stations increased they found higher correlations for stations oriented in a SW-NE direction than for other bearings.

Sneva and Hyder (1962a) developed a method of forecasting production of rangeland grasses for a given year when present CY precipitation was expressed as a percentage of the median CY precipitation for a related weather monitoring station. The CY avoids the two summer months of July and August when typically scant or isolated precipitation has little effect on vegetative production. Kindschy (1982) developed a somewhat similar method, for forecasting the production of forage shrubs in southeastern Oregon, based upon the ratio of the present CY precipitation to the accumulative mean CY precipitation. The accumulative mean was calculated through the inclusion of present CY precipitation data each year. Prior means were not dropped with the addition of new means. The influence of short-term wet or dry cycles was thus smoothed.

Methods and Results

Crop year precipitation data for seven permanent recording stations in Malheur County, Oregon, were analyzed for the 13 year period 1966-78. Elevation above sea level for each station was compared to precipitation received during the CY through linear regression analysis. A strong correlation ($r = 0.938$, $P < .01$) was found between station elevations and precipitation received during the crop year. The resultant equation was:

$Y = 0.0115\ X + 12.532$

. . . where Y is crop year precipitation in centimeters and X is station elevation in meters.

Sneva and Hyder (1962) calculated current CY precipitation as a percentage of the median CY precipitation in order to forecast perennial grass production during the subsequent growing season. I employed a similar calculation for adjustment of the regression equation to the present crop year. Comparison of the median CY precipitation data with that of the mean for the period showed nearly identical values ($\pm$ 3.6 percent). I selected the accumulative mean due to its ease of calculation and familiarity to users (Table 2).

TABLE 2. Ratio of CY precipitation for the years 1979-1982 at NOAA weather stations in northern Malheur County, Oregon. Present CY precipitation ÷ accumuative mean CY precipitation of each station.

NOAA Station	Elevation (m)	1979	1980	1981	1982
Sheaville	1,408	1.05	1.26	1.39	2.00
Beulah	997	.90	1.36	1.25	1.65
Vale	683	.94	1.25	1.29	1.48
Westfall	957	.97	1.34	1.38	1.58
Danner	1,288	.96	1.00	1.31	1.41
Rockville	1,119	.95	1.31	1.50	1.23
Juntura	863	.92	1.49	1.18	1.47

Combining the CY adjustment factor with the regression equation provided the following formula for forecasting the amount of CY precipitation at sites of known elevation within the polygon of influence of a NOAA station:

Metric data:

$$\text{CY Precip.} = [(0.0115 \times \text{Elev (m)}) + 12.532] \times \frac{\text{Present CY Precip (cm)}}{\text{Mean CY Precip (cm)}}$$

English data:

$$\text{CY Precip.} = [(0.0014 \times \text{Elev (ft)}) \times 4.941] + \frac{\text{Present CY Precip (in)}}{\text{Mean CY Precip (in)}}$$

(where the present CY precipitation and the mean CY precipitation pertain to the NOAA station within the polygon.)

During 1978, the Bureau of Land Management placed 15 additional precipitation gauges in remote sites within the study area (Fig. 1). It was felt that the distribution of existing NOAA stations was too sparse and non-uniform to allow adequate forecasting of CY precipitation required by Sneva's method of predicting production of perennial grass forage. Information on the correlation of the newly gathered precipitation data to

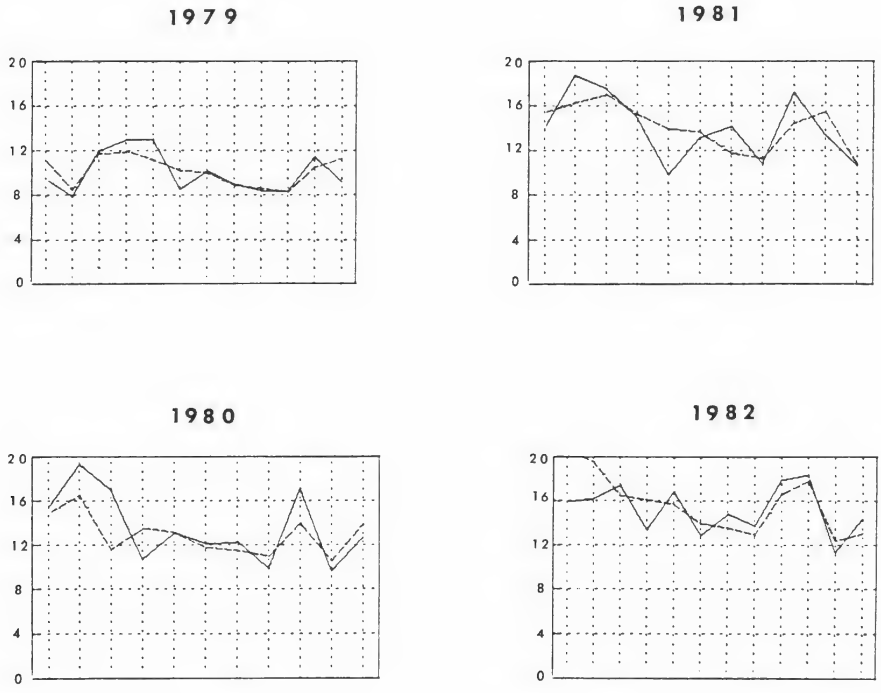

Figure 2. Comparison of the amount of CY precipitation received (solid line) with amount predicted. Horizontal axis represents individual BLM gauging sites.

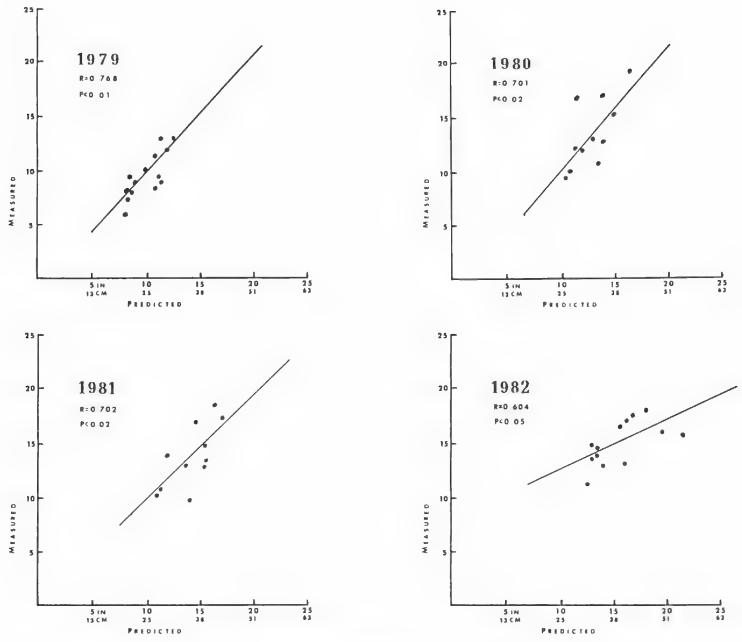

Figure 3. Correlation of predicted to measured CY precipitation.

that from existing NOAA stations would enable refinement of local Thiessen polygon boundaries (Sneva and Calvin 1978). If correlations were sufficiently strong, the new BLM gauges could be abandoned and NOAA data used to forecast subsequent vegetative production.

Crop year precipitation for 1979, 1980, 1981, and 1982 were obtained from these new sites. Each year one or more of the new gauges suffered vandalism or other disruption causing a loss of data. Valid information was obtained for 14 gauges in 1979, 11 during 1980, 11 during 1981, and 13 during 1982. These data were compared to precipitation predicted by the modified regression equation (Fig. 2).

Individual gauge measurements were plotted for each year for comparison with CY precipitation amounts predicted through application of the modified regression equation. Figure 3 illustrates the relationship of measured precipitation to predicted precipitation.

Field Application

A rangeland manager wishes to determine the approximate crop year precipitation for a newly seeded experimental plot at 1,300 m elevation. The plot is located within the polygon of the Vale NOAA station. The accumuative mean CY precipitation for Vale is 22.48 cm. During the 1982 CY (September 1981 through June 1982) the Vale station measured 33.30 cm of precipitation. Thus the adjustment factor for 1982 at Vale is $33.30 \div 22.48 = 1.48$. Applying the equation:

$$\begin{aligned}\text{CY Precip.} &= [(0.0115 \times \text{Elev.}) + 12.532] \times \text{CY Adjustment Factor} \\ &= [0.0115 \times 1300) + 12.532] \times 1.48 \\ &= 40.7 \text{ cm precipitation}\end{aligned}$$

Literature Cited

Helvey, J D., and W. B. Fowler. 1982. Precipitation variability in the Columbia Basin of Washington. Northw. Sci. 56: 27-33.

Henry, A. J. 1919. Increase of precipitation with altitude. Mon. Weather Rev. 47: 33-41.

Kindschy, R. R. 1982. Effects of precipitation variance on annual growth of fourteen species of browse shrubs in southeastern Oregon. J. of Range Management 35: 265-266.

Lull, H. W., and L. Ellison. 1950. Precipitation in relation to altitude in central Utah. Ecology 31: 479-484.

Sneva, F. A., and L. D. Calvin. 1978. An improved Thiessen grid for eastern Oregon. Agric. Meteorol. 19: 471-483.

———, and D. N. Hyder. 1962a. stimating herbage production on semiarid ranges in the Intermountain Region. J. Range Management 15: 88-93.

Received, May 3, 1983
Accepted for publication, February 28, 1984

Jack H. Woods[1]

George M. Blake

School of Forestery
University of Montana
Missoula, Montana 59812

and

Fred W. Allendorf

Department of Zoology
University of Montana
Missoula, Montana 59812

Using Isozyme Analysis to Aid in Selecting Genetically Superior Ponderosa Pine for Coal-Mine Spoil Reclamation

Abstract

Isozyme analysis was used to investigate the genetic population structure of ponderosa pine from the Colstrip area in eastern Montana. Results are discussed in terms of designing a progeny test to select trees which produce seedlings with a superior ability to survive on regraded coal-mine spoils. It is estimated that selection of 75 parent trees divided among 5 stands will efficiently sample the genetic diversity present. Due to the natural stand history, a large amount of gene flow between stands and the relatively small area being reforested, gene conservation is not of concern. As a result, the three or four parent trees whose progeny have the best survival rates can be used for future seed collection. Selection of three or four trees should allow a large genetic gain even though only 75 parents are being tested.

Introduction

Mine-spoil reclamation has become important in many parts of the world in recent years. Local laws often require that native species be established, and that the productivity of reclaimed land be equal to or greater than what it was before mining. Most research effort is put towards the engineering problems of regrading the spoils to create a medium suitable for the desired plant species, or towards the cultural techniques of seeding and planting. Fewer studies have investigated the potential for intraspecific selection of plants exhibiting genetic superiority in survival or growth on the reclaimed sites.

Most plant species show a great deal of variability that can be attributed to genetic differences among individuals. This variability has been used in agriculture, horticulture and forestry in selecting and breeding lines considered superior for the specific improvement objectives. In reclamation work, Plass (1969) found a great deal of variation among open-pollinated families of Virginia pine (*Pinus virginiana*) in their ability to survive on acid surface-mine spoils. Certain hybrid poplar clones have also shown superior survival ability on mine-spoils (Jones 1973, Davidson 1980). Geographic location of the seed source has been found to influence a plant's ability to survive on mine-spoils for alder (*Alnus glutinosa*) (Funk 1973), Austrian pine (*Pinus nigra*)

[1]Currently with Cowichan Lake Research Station, British Columbia Ministry of Forests, Box 335, Mesachie Lake, B.C. VOR 2NO, Canada.

(Neys and Cech 1977), and several species of birch (*Betula* spp.) (Davidson 1977). Scanlon (1979) reports differential survival and growth on mine-spoil sites among families for various shrub species. Taxonomic lines within a number of plant species have also been found to exhibit varying abilities to survive on soils with high heavy-metal concentrations (Antonovics *et al.* 1971).

Plants of high genetic quality, in terms of survival on mine-spoil areas, could provide economic benefits for reclamation efforts in two ways: 1. increased survival for a normal amount of site treatment and planting expense, or 2. satisfactory survival for less than normal site treatment and planting expense.

At Colstrip, in southeastern Montana, large tracts of land are being strip-mined for coal. The dry climate in this area hinders reclamation efforts, although reasonable success has been achieved with grass and shrub species. Indigenous ponderosa pine (*Pinus ponderosa* var. *scopulorum*) is generally limited to rocky upland sites (Richardson 1981), and preliminary efforts to establish this species on regraded mine-spoils have failed (MSU 1978).

To insure a high genetic quality in seed being used for reforestation efforts, a selection program is being carried out to identify open-pollinated ponderosa pine families that exhibit a superior ability to survive on mine-spoil areas. (Mine-spoils used in this study consist of soils that are reconstructed and graded as the first stage of reclamation.) This paper describes the use of isozyme analysis to estimate the amount and distribution of genetic variation in ponderosa pine from the Colstrip area, and its application to the selection of parent trees.

Isozyme Analysis

The use of electrophoresis to estimate certain genetic characteristics of populations has become widespread since the late 1960's. The technique uses an electric current to separate enzyme proteins in a gel medium. An enzyme is coded by the DNA found at certain chromosome locations (loci); the various forms of an enzyme coded at different loci are called isozymes. Isozyme variants result when alternate gene forms (alleles) are found at a chromosome locus. The isozyme variants will often migrate at different rates through the gel. Following electrophoresis, the gel is stained for the desired enzymes; isozyme variants can be detected by their location on the gel. (See Harris and Hopkinson (1976) for detailed procedures). Data from isozyme analysis allows accurate estimates of genetic variation and other genetic characteristics.

In conifers the amount and distribution of genetic diversity in quantitatively measured growth characteristics is reflected in estimates from isozyme analysis. Ponderosa pine from the northern Rocky Mountains exhibits a great deal of isozyme variation, with about 88 percent of the variation being due to genetic differences among individuals within a stand, and 12 percent due to differences among stands (O'Malley *et al.* 1979). This result is in general agreement with a study by Madsen and Blake (1977) which attributes 28.5 percent of the genetic variation in two year height growth to differences among stands. Most coniferous species exhibit a large amount of isozyme variability as well as a great deal of variability in quantitative characteristics. However, species such as red pine (*Pinus resinosa*) (Fowler and Morris 1977, Allendorf *et al.* 1982) and western red cedar (*Thuja plicata*) (Copes 1981) exhibit very little genetic variation in quantitative characteristics, and have also shown little isozyme variability.

Isozyme analysis offers a fast and inexpensive method of estimating the genetic structure of populations. This is basic but important knowledge which can improve the efficiency of a program aimed at selecting and breeding for the genetic improvement of a characteristic.

Methods

Ponderosa pine in the Colstrip area is generally found in small stands isolated by grasslands. To investigate the amount and distribution of genetic variation in these isolated ponderosa pine stands, open-pollinated seeds were collected from 50 trees throughout each of 6 stands. The stands were separated by varying distances ranging from 0.9 to 13.6 kilometers. Stand areas and densities are shown in Table 1.

TABLE 1. Size, area, density, and genetic heterozygosity (He) for six ponderosa pine stands sampled near Colstrip, Montana.

Stand	Number of trees*	Area (hectares)	Trees per hectare	He (percent)
1	260	4.4	59	12.8
2	320	3.1	74	13.2
3	920	8.4	110	12.7
4	400	3.4	118	11.5
5	2550	12.4	181	10.4
6	225	5.2	43	13.9
			All stands combined	He = 12.6

*Number of trees of reproductive age estimated from air photos.

To estimate allele frequencies in the present stands, as well as genotype frequencies in the seed crops, one seed from each tree was screened for isozyme variants in megagametophyte and embryo tissue over 23 isozyme loci. Fresh ponderosa pine seeds from the Colstrip area do not require stratification (Woods and Blake 1981), therefore, seeds were soaked in water for 18 hours and germinated at room temperature on moist filter paper. Megagametophytes and embryos were dissected from the seeds, when the radicle had extended about one centimeter, and were crushed in 0.2 to 0.5 ml of distilled water in proportion to the amount of tissue present. Homogenate from the megagametophyte and embryo of each seed was absorbed into filter paper wicks and placed separately in a starch gel for electrophoresis.

Electrophoretic methods, enzymes, and allelic variants are described by Woods *et al.* (1983). Enzyme stains are described by Allendorf *et al.* (1977). For a general description of electrophoretic techniques in conifers see Conkle (1972).

Results

The amount of genetic variation, as estimated from isozyme analysis, is generally expressed as the average proportion of loci per individual (seed) exhibiting more than one electrophoretically detectable isozyme allele. This ratio is called the genetic heterozygosity (*He*). Values of *He* for individual stands varied from 10.3 to 13.7 percent, with an average over all stands of 12.6 percent (Table 1). No significant (prob. > 0.05) differences in *He* were found among stands.

The amount of genetic heterozygosity in ponderosa pine from the Colstrip area

(12.6 percent) is lower than for ponderosa pine from the northern Rocky Mountains in the U.S. (18.6 percent) (Allendorf *et al.* 1982). It is also lower than the average for 20 coniferous species (20.7 percent) compiled by Hamrick *et al.* (1981) (see Fig. 1). However, levels of *He* in Colstrip pine are high relative to many plant and animal species, and also to some conifer species, indicating that considerable genetic variation exists in these populations.

The genetic heterozygosity in populations can be partitioned into the amount of genetic diversity within subpopulations (stands) and the genetic diversity which is due to differences among subpopulations (Nei 1973). In the Colstrip pine stands, an average of 98.5 percent of the genetic heterozygosity is found within individual stands and 1.5 percent is due to differences among stands. Although the 1.5 percent is small, significant gene frequency differences exist among stands at some loci.

Discussion

In order for tree improvement to be successful, genetic variation must be present in the species and populations from which parent trees are chosen. Isozyme analysis indicates that ponderosa pine in the Colstrip area is genetically variable, and local populations will likely provide the variation needed for improvement. Without sufficient variation

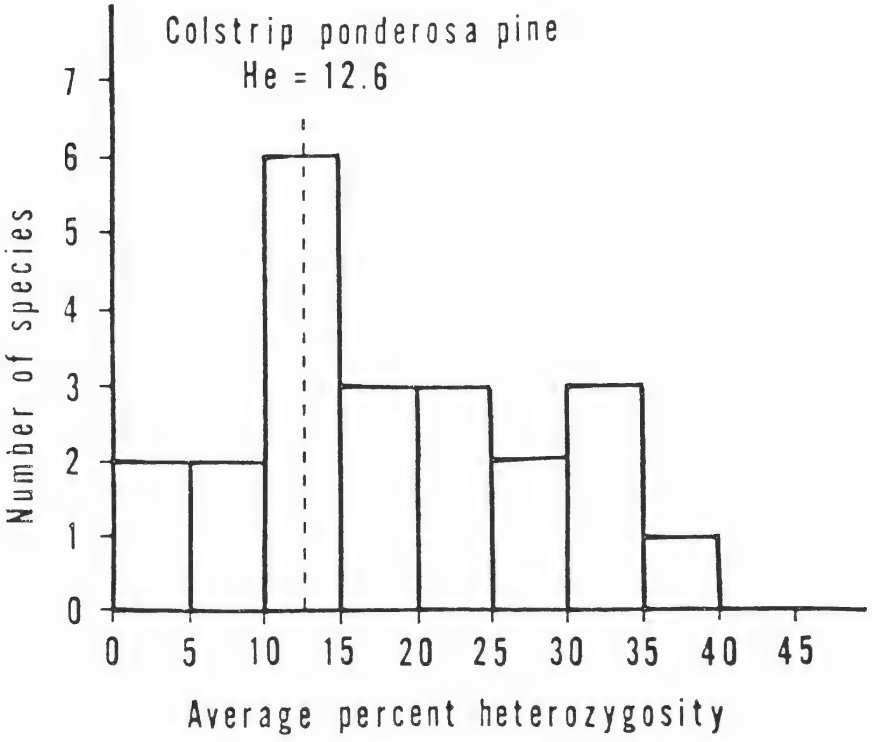

Figure 1. Distribution of the average heterozygosity (He) found in 22 conifer species (data from Hamrick *et al.* 1981).

in local stands, seed would have to be collected over a large geographic area to obtain the variable genotypes needed. Using local trees as progeny test parents, avoids the survival and growth problems often encountered when seed is moved from its natural origin. Also, the use of local trees involves less time and expense in seed collection and maintenance of selected parents.

Selection of Parents for Progeny Testing

In most tree improvement projects, parent trees with the desired phenotype (i.e., rapid volume growth, straight bole, etc.) are selected from natural stands. If progeny from these parents also exhibit these traits, then an initial genetic gain is made from the phenotypic selection. The trait of mine-spoil survival is not exhibited by a naturally occurring tree, therefore parents cannot be selected on this basis. To determine which parent trees produce progeny most able to survive on regraded mine-spoils, seedlings from various trees must be planted in an appropriate design, and survival rates determined (progeny test). On the basis of progeny survival, parent trees can then be selected for operational seed collection and, if desired, future breeding. Timber production is not the objective of this mine-spoil reforestation, therefore selection for traits such as rapid height growth is not of concern for this study.

Since parent trees cannot be chosen on the basis of their phenotype, it is desirable to choose parents which will represent a cross section of the genetic variation present in local stands. Isozyme analysis indicates about 98.5 percent of the genetic diversity exists within a stand. Therefore, by choosing parent trees from a single stand, genotypes will be drawn from a pool containing all but 1.5 percent of the genetic variation. Significant genetic differences also exist among stands, however, so by sampling parent trees from a number of stands a more diverse cross section of genotypes can be included (Brown 1978). Isozyme analysis results allow parent trees to be chosen in a design that efficiently samples the local genetic diversity.

Seed production varies among trees in ponderosa pine. Open-pollinated seed is used to produce seedlings for the progeny test, so good seed production is necessary to select parent trees. Parents producing progeny with superior survival ability will be used for future operational seed collection. If seed production is heritable, then trees from selected parents established on mine-spoils will also be good seed producers and stands are more likely to become self-regenerating.

Selection of Genetically Superior Trees

Following the progeny test, parent trees whose progeny had the best survival rate on the mine-spoils will be chosen for future seed production. The amount of genetic gain (G) achieved by selecting these parents is dependent upon selection differential (S) and the degree to which a trait is passed from parent to offspring (heritability = h): $G = Sh$. Selection differential is a measure of the difference between the average progeny survival rate over all parents and the average survival rate of progeny from the best selected parents. The fewer number of best parents chosen, the higher the selected average and the greater the selection differential and genetic gain.

Generally in tree improvement work, gene conservation is of concern (Adams 1981). Large scale forestery operations may significantly alter the genetic resource; measures are required to minimize the loss of genetic diversity. A trade-off is reached

between conserving a reasonably large superior population and genetic gain. In order to achieve a large selection differential, as well as to maintain a sufficient number of superior trees, many individuals (300-1000) are usually tested and the best 40 or 50 selected for a breeding population.

The conservation of genotypes, by selecting a large number of superior parents from progeny test results, is considered unnecessary in this project for the following reasons:

1. Strip-mine spoil reforestation involves small areas of land (relative to the areas reforested in large-scale forestry operations), and only small patches will be reforested, with most areas being reclaimed to grasslands.
2. Open-pollinated families will be used, therefore, even with a small number of female parents, a large number of male parents will be included.
3. Areas will only be mined and reforested once, and stands will regenerate naturally after they are established. Isozyme analysis indicates a great deal of pollen movement takes place between stands (Woods *et al.* 1983), causing a broadening of the genetic base in future generations.
4. The natural fire history of ponderosa pine in the Colstrip area indicates it is common for stands to originate from a small number of parents (Richardson 1981).

Selection of three or four parent trees with the best progeny survival should be sufficient to meet seed requirements. By selecting such a small number of genetically superior trees, a high selection differential and genetic gain should be obtained from a progeny test involving a small number of parents. For this project, a progeny test involving 75 parent trees, selected over 5 different stands (15 per stand), is considered sufficient to achieve a large genetic gain, while keeping the investment in seed collection and progeny testing small.

In the Colstrip area, obtaining a high survival rate of seedlings planted on minespoils is the main objective; wood volume production is of little concern. Seedling mortality is highest following planting, and the success or failure of a seedling will likely be determined within one or two years. This is a great advantage in terms of parent tree selection. The short period of time required to obtain results means that the investment in progeny testing need only be carried on for one or two years before superior seed can be used operationally.

Acknowledgements

Funding for this study was provided by Western Energy Company from Colstrip, Montana.

Literature Cited

Adams, W. T. 1981. Population genetics and gene conservation in Pacific Northwest conifers. Pp. 401-405, *In* G. G. E. Scudder and J. L. Reveal (eds.), Evolution Today, Proc. of the Second International Congress of Systematic and Evolutionary Biology.

Allendorf, F. W., K. L. Knudsen, and G. M. Blake. 1982. Frequencies of null alleles at enzyme loci in natural populations of ponderosa and red pine. Genetics 100:497-504.

———, N. Mitchell, and N. Stahl. 1977. Isozyme loci in brown trout (*Salmo trutta* L.): detection and interpretation from population data. Hereditas 86:179-190.

Antonovics, J., A. D. Bradshaw, and F. G. Turner. 1971. Heavy metal tolerance in plants. J. B. Cragg (ed.), Adv. in Ecol. Res. 7:1-85.

Brown, A. H. D. 1978. Isozymes, plant population genetic structure and genetic conservation. Theor. and Appl. Genet. 52:145-157.

Conkle, M. T. 1972. Analyzing genetic diversity in conifers . . . isozyme resolution by starch gel

electrophoresis. U.S. Dept. Agric. Forest Serv. Pacific South-West Forest and Range Exp. Sta. Res. Note PSW-264.
Copes, D. L. 1981. Isoenzyme uniformity in western red cedar seedlings from Oregon and Washington. Can. J. Forest Res. 11:451-453.
Davidson, W. H. 1977. Birch species survive well on problem coal mine spoils. Pp. 95-101, *In* Proc. of the 24th Northeastern Forest Tree Improvement Conference, 1976. College Park, Maryland.
———, 1980. Hybrid poplars for spoil reforestation. Proc. of the American Council for Reclamation Research, 1980. Wheeling, West Virginia. Abstract in Reclamation Review 3:241.
Fowler, D. P., and R. W. Morris. 1977. Genetic diversity in red pine: evidence for low genetic heterozygosity. Can. J. Forest Res. 7:343-347.
Funk, D T. 1973. Growth and development of alder plantings on Ohio stripmine banks. Pp. 483-491, *In* Ecology and Reclamation of Devastated Land. Gordon and Breech, London.
Hamrick, J. L., and J. B. Mitton, and Y. B. Linhart. 1981. Levels of genetic variation in trees: influence on life history characteristics. Pp. 35-41, *In* M. T. Conkle (ed.), Proc. of the Symposium on Isozymes of North American Forest Trees and Forest Insects. Berkeley, Calif. 1979. U.S. Dept. Agric. Forest Serv. Pacific Southwest Forest and Range Exp. Sta. Gen. Tech. Rep. PSW-48.
Harris, H., and D. A. Hopkinson. 1976. Handbook of Enzyme Electrophoresis in Human Genetics. American Elsevier, New York.
Jones, W. G. 1973. Hybrid poplar plantings on strip-mine sites in Pennsylvania. Pp. 160-163, *In* Proc. of the 20th Northeastern Forest Tree Improvement Conference, 1972. Durham, New Hampshire.
Madsen, J. L., and G. M. Blake. 1977. Ecological genetics of ponderosa pine in the northern Rocky Mountains. Silvae Genet. 26:1-8.
MSU. 1978. Ponderosa pine planting study. Pp. 27-31, *In* Research on Revegetation of Surface Mined Lands at Colstrip, Montana; Progress Report 1975-77. Montana Agric. Exp. Sta. Res. Rep. 127. Montana State Univ., Bozeman, Montana.
Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. 70:3321-3323.
Neys, R. N., and R. C. Cech. 1977. Evaluation of Austrian pine seed sources on amended and unamended strip-mine spoils. Pp. 104-116, *In* Proc. of the 25th Northeastern Forest Tree Improvement Conference. 1975. Orono, Maine.
O'Malley, D. M., F. W. Allendorf, and G. M. Blake. 1979. Inheritance of isozyme variation and heterozygosity in *Pinus ponderosa*. Biochem. Genet. 17:233-250.
Plass, W. T. 1969. Genetic variability in survival and growth of Virginia pine planted on acid surface-mine spoils. Pp. 493-501, *In* F. J. Hutnik and G. Davis (eds.), NATO Advanced Study Institute on the Ecology and Revegetation of Drastically Disturbed Areas. Vol. 1. Pennsylvania St. Univ.
Richardson, N. E. 1981. Stand Structure and Patterns of Conifer Regeneration Near Colstrip, Montana. Univ. of Montana. M.S. Thesis.
Scanlon, D. H. 1979. Genetic improvement of wildlife shrubs for disturbed sites. Proc. of the American Council for Reclamation Research. 1979. Oak Ridge, Tennessee. Abstract in Reclamation Review 2:44.
Woods, J. H., and G. M. Blake. 1981. Effects of stratification on *Pinus ponderosa* (var. *scopulorum* Engelm.) seed from Colstrip, Montana. Montana Forest and Conservation Exp. Sta. Missoula, Montana. Res. Note 18.
———, and F. W. Allendorf. 1983. Amount and distribution of isozyme variation in ponderosa pine from eastern Montana. Silvae Genet. 32:151-157.

Received May 26, 1983
Accepted for Publication March 1, 1984

Maurice J. Mundorff[1]
1428 Sea Cliff Dr. NW.
Gig Harbor, Washington 98335

Glaciation in the Lower Lewis River Basin, Southwestern Cascade Range, Washington

Abstract

In pre-Fraser time, accumulation of ice in the upper Lewis River basin became so extensive that a large ice-tongue extended down valley and spread widely in the lower Lewis River Basin, reaching to within about 8 km of the present route of Interstate Highway I-5. The ice-tongue, more than 600 m thick at Cougar, spread across Chelatchie Prairie and into the East Fork Lewis River basin, extending down that valley to near Battle Ground. The ice also flowed up Canyon and Siouxon Creeks, and the East Fork Lewis River. Extensive deltaic and ponded outwash deposits were formed at many places. Other features of the glaciation include boulder trains, erratic boulders, and rock drumlins. Glacial-caused drainage changes include changes in the course of the East Fork Lewis River and Canyon Creek. Although more than one glacial advance may be represented, the majority of the deposits appear to represent a single glacial episode. Carbon-14 dating of wood from the ponded deposits indicates that they are more than 60,000 years old. The depth of weathering and rind thickness suggest that the glaciation occurred in late Pleistocene time, considerably before the Fraser glaciation.

Younger, Fraser-age glaciers originated in cirques with floors at altitudes of 825 to 915 m at the heads of many drainages in the Canyon and Siouxon Creek basins. These glaciers deposited till and moraine at altitudes ranging down to about 460 m.

Introduction

During the course of a ground-water investigation in Clark County, 1949-1954, deposits of glacial drift were mapped in the northern part of the county. The deposits are described briefly (Mundorff 1964), and their extent is shown on Plate 2 of that report. This paper gives the results of a much more detailed study of these glacial deposits.

The extensive glacial deposits in the lowlands of the Lewis River basin suggest that glaciers were widespread on the western slopes of the Cascades in southern Washington, yet there have been no previous detailed studies of glaciation in the area. In his summary of the glacial history of western Washington and Oregon, Crandell (1965), does not mention any glaciation in the area. In describing pyroclastic flows and lahars, Hyde (1975) briefly discusses Fraser-age glaciation on the south flank of Mount St. Helens. Since the beginning of the present study, Crandell (1979) has described a number of occurrences of Fraser-age and pre-Fraser age drift around the base of Mount St. Helens. Hammond (1980) shows six small areas of Hayden Creek Drift in the Canyon and Siouxon Creek drainages. However, the western limit of his map is longitude 122°18′45″ and it does not show the lower reaches of the Lewis River Basin.

Areal Extent and General Features of the Amboy Drift

Glacial drift including till, lacustrine and fluvial outwash deposits, ice-contact deposits, and boulder deposits occurs along the Lewis River valley, East Fork Lewis River valley,

[1]Retired from the U.S. Geological Survey.

and on most of the interfluves between the two rivers (see Fig. 1). These glacial deposits are named the Amboy Drift for their characteristic exposure in the vicinity of the town of Amboy. The western margin of the till extends northwest from the East Fork Lewis River near Lewisville Park (altitude 90 m), to the south flank of Bald Mountain (altitude 275 m), around the east end of that mountain, and down the Lewis River to within 8 km of Interstate Highway I-5 (altitude 60 m). Generally the terminus

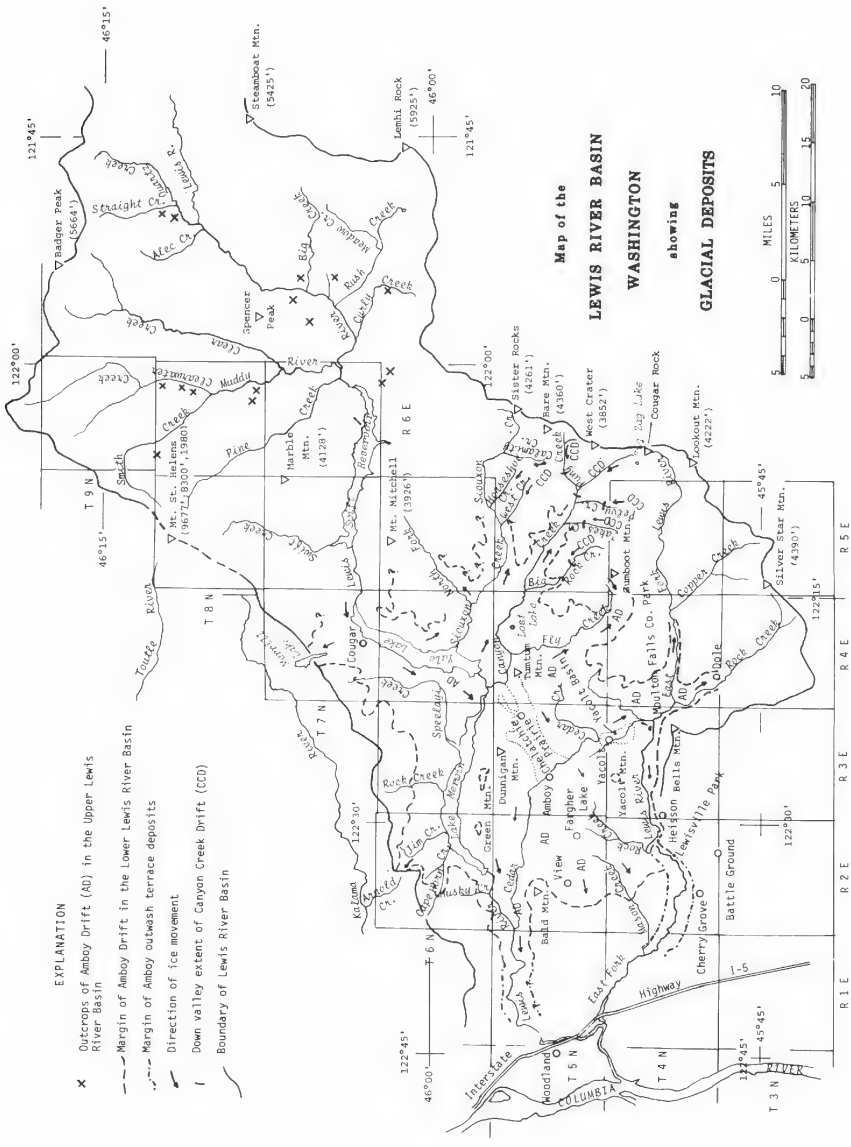

Figure 1. Map of the Lewis River Basin, Washington showing glacial deposits.

was deliniated on the basis of the westernmost exposures seen and, where till was not exposed, boulders in the soil were assumed to indicate that till underlay the surface.

Originating in the upper Lewis River Basin, a large ice tongue came down valley, reaching an altitude of about 760 m near Cougar. Down valley the ice spread widely; lobes of ice moved west, southwest, south, southeast, and east. Between the north flank of the Lewis River valley and the south side of the East Fork Lewis River valley, only the top of Yacolt Mountain and two small areas on Green Mountain were not overridden by the ice. The ice reached 560 m at the east end of Green Mountain and about 420 m on the north flank of Yacolt Mountain. A lobe of the glacier moved southeast and east up Canyon and Siouxon Creeks. Farther south one tongue of ice flowed down, and another flowed up the East Fork of Lewis River.

East of Chelatchie Prairie the ice over-rode the upland in the Cedar Creek drainage, reaching an altitude of about 610 m on the flanks of a steep hill 0.5 km north of Cedar Creek in sec 28, T 5 N, R 4 E. In the Fly Creek drainage, till was found at many places between altitudes of 550 and 640 m. Projection of inferred slopes of the drift margin suggest that the Amboy Drift could not have extended south along Fly Creek beyond about the southern boundary of T 5 N, at an altitude of about 565 m. Several excellent exposures of till and widespread boulders and cobbles are found farther south to altitudes of 640 m. The till is identical in appearance to the Amboy Drift, but is believed to have been deposited by a local glacier that may have originated on the southwest flank of Gumboot Mountain.

Ice extended up Canyon and Siouxon Creek valleys, and excellent exposures of drift are found at many places. Amboy age drift is exposed almost continuously up Canyon Creek to and beyond Pelvy Creek. However, considering the probable slope of the ice surface, it is unlikely that the Amboy ice lobe extended as far up valley as that creek. The drift in the reach above the mouth of Pelvy creek must have been deposited by contemperaneous local glaciers which occupied Canyon and tributary valleys. In some of these valleys there is an unglaciated section between the Amboy Drift deposited by the Lewis River ice lobe and the drift deposited by ice of local origin, but in the Canyon Creek valley ice from the two sources apparently merged. The two drifts are indistinguishable.

Exposures of till were found in Siouxon Creek valley at altitudes up to at least 730 m and possibly 850 m. Drift found above 580 to 600 m probably was deposited by ice moving down the Siouxon valley from sources in the headwaters of that drainage.

North of Lewis River, till is exposed at many places along highway 503. Glacial drift crops out in the drainage of Cape Horn Creek to an altitude of 490 m. Till also is exposed at several places along Dubois Road, near Jim Creek. The divide at the end of the road, between Jim Creek and Arnold Creek (which drains into Kalama River), is at an altitude of about 335 m; ice must have spilled through this gap. Eastward, in the Rock Creek and other drainages, till occurs to an altitude of 490 m. Considering the slope of the ice margin, the drift probably reached an altitude of about 550 m in that area. North of the town of Cougar, glacial drift is exposed along the road between Cougar and Merrill Lake, and on a bench east of the lake, at an atitude of 640 m. About 3.5 km southeast of Cougar, Amboy Drift occurs at an altitude of nearly 760 m and the ice probably reached that altitude in the vicinity of Merrill Lake. Because the present divide between the Lewis and Kalama Rivers is less than 490 m in altitude, ice either

moved north through the gap, or the Kalama valley was already occupied by an ice lobe and the two lobes merged. Amboy-age drift is exposed at several places on the west flank of Marble Mountain at altitudes of 900 to 1035 m; however, this drift was deposited by local ice.

Many outcrops of Amboy Drift, including several exposures along Clearwater Creek, were found in the Muddy River drainage. Outcrops of thin-bedded clays and sands were found at locations 180 to 240 m above the present valley floors, indicating temporary ponding.

Amboy Drift was found to altitudes of 760 m south of the head of Swift Reservoir; it probably extends considerably higher. East of the reservoir, drift was seen at many places both north and south of the Lewis River. Drift of two or more ages is represented; some of the deposits are Amboy Drift, but other exposures obviously are younger and probably are of Fraser age. The distribution of the exposures and of glacial lakes on the upland (see 7½-minute Lone Butte Quad.) indicates that nearly the entire upland south of the Lewis River was ice-covered and served as a gathering ground for the glacier that deposited the Amboy Drift in the lower Lewis River Basin.

Depositional Features of the Glacial Deposits

The Amboy Drift includes till, coarse deltaic outwash, fine-grained thin-bedded deposits that accumulated in ponds and as ice-contact deposits, boulder trains and nests, and individual boulders.

Till forms a discontinuous blanket over most of the area. The Amboy till varies considerably, but almost everywhere contains large amounts of pebbles, cobbles, and boulders in a clayey and gritty matrix. The unweathered till is blue or gray; the upper 1.5 to 2 m is weathered to various shades of brown. At many places the till is thin and is oxidized to the base. Till a few feet below the surface is tough and difficult to dig; fresh till is exceedingly tough.

Boulders commonly are 0.3 to 0.5 m in diameter, but boulders to 1 to 1.5 m were seen at many locations. The clasts comprise a wide variety of volcanic materials including fine- to medium-grained basalt and andesite, rhyolite, dacite, and gray porphyritic lava. Equigranular granitic and dioritic rocks were found in many outcrops.

In the uplands north and west of Yacolt Mountain, and in some other areas, some till outcrops have a much larger proportion of brown clayey material. As shown by soils in adjacent non-glaciated areas, there was a well developed pre-glacial soil 4.5 to 6 m deep in this area, and as the ice advanced, debris carried by the ice was mixed with this soil, giving the till a false appearance of a thick soil profile. For the last few miles of the glacial advance, west of Fargher Lake, the ice overrode the Troutdale Formation and incorporated material from that unit, including quartzite pebbles and some deeply weathered volcanic and granitic stones, into the till.

The thickest section of till, about 30 m, was measured on the north side of the East Fork Lewis River, about 6.5 km north of Battle Ground.

Because, at many places, especially at lower elevations, the ice incorporated such a large amount of pre-weathered material into the till, it is difficult to get an accurate idea of the depth and degree of weathering that has occurred since glaciation. Generally, the till appears to be much more deeply weathered than the Vashon till of the Puget Sound area; oxidation to depths of 1.5 to 2 m is usual. Some pebbles have weathered

rinds several mm thick, yet in the same outcrops many pebbles of the same types of rocks have rinds less than 1 mm thick.

Outwash deposits underlie much of the surface of Chelatchie Prairie and the Yacolt Basin. At an industrial supply well 1.5 km east of Chelatchie, the valley fill is 66 m thick, of which probably only the upper 20 to 30 m is of glacial origin. Another well, about 2.4 km down Cedar Creek from Amboy, penetrated 39 m of drift and alluvium before entering volcanic rock at an altitude of about 70 m. This well was drilled only about 180 m from a now abandoned and overgrown gravel pit in glacial outwash. (Mundorff 1964, Fig. 15)

Yacolt Basin, about 60 m higher than Chelatchie Prairie, also is underlain by outwash and till. Reworking of this material by glacial meltwater has left a lag covering of boulders over the basin. A well drilled for the town of Yacolt, on the west side of the basin, penetrated 35.4 m of glacial deposits and alluvium before entering volcanic rock at an altitude of about 178 m.

East Fork Lewis River occupies a flat-floored valley beginning at a point about 2.5 km west of the south end of the basin. The valley-floor deposits consist of glacial outwash and till. These deposits continue down valley to Lewisville Park, and an outwash terrace deposit extends downstream for another 8 km. The terrace deposit is well exposed along the south side of the East Fork Lewis River, northeast and northwest of Cherry Grove. Near the center of sec. 28, T 4 N, R 2 E, a borrow pit in the edge of the terrace exposes more than 9 m of poorly sorted, crudely stratified outwash containing a wide variety of rock materials ranging in size from sand to large boulders. One lens of iron-stained sand is 75 to 90 cm thick and about 12 m long. Exposures of the outwash terrace deposits were found downstream as far as Mason Creek.

The Amboy outwash terrace deposits overlie the Troutdale Formation along the East Fork Lewis River at elevations 24 to 27 m above the present floodplain. Similar outwash terrace deposits were found along Lewis River, where the base of the deposits also appears to be about 25 m above the present floodplain, and it seems probable that the local base level was that much higher in Amboy time than now.

A thick section of deltaic outwash is exposed in a road cut 7.5 to 9 m high along Canyon Creek in the SW¼ sec 1, T 6 N, R 4 E, at an altitude of 350 m, nearly 120 m above Canyon Creek. Thick sections of deltaic outwash are found at several other places along Canyon Creek, and also on the south flank of Dunnigan Mountain at an altitude of 340 m. Small lenses of stratified drift were seen at many other places in upland areas, usually overlain by till.

Thin-bedded lenticular deposits of stratified clay, silt, and fine- to medium-grained sand occur at many places. In some exposures the sediments are folded, apparently from loading by over-riding ice. A common feature is the presence of scattered pebbles, probably dropped from floating blocks of ice.

The deposits generally occur as lenses, at many places the complete lens can be seen entirely enclosed in till, but at other places only part of the lens is exposed. Lenses range from less than 0.3 m thick and 1 m long to 3 m thick and 12 to 15 m long.

The most extensive and thickest ponded deposits occur along Canyon Creek and are exposed in cuts along Forest Service Road N54. At least 10 such outcrops occur along the road, ranging in altitude from about 245 to more than 520 m, and from 60 to 150 m above present stream level. Thick outcrops begin at a point about 4.6 km east

of the first bridge across Canyon Creek and continue intermittently for 3.5 km as the road rises from an altitude of 270 to 385 m. Six separate outcrops, ranging from 3 to 9 m thick, were found in this interval. The deposits either were capped by till, or till was found at a higher level up valley. As the ice lobe moved up valley it blocked the Canyon Creek drainage at progressively higher levels, with ponds forming at the head of the ice tongue. A cumulative total of at least 33 m of finely laminated clay and sand was deposited in front of the ice in this 3.5 km reach. The deposits consist of alternating layers of clay and fine- to medium-grained sand. Clay layers range in thickness from 2 to 15 mm and average about 5 mm. The sand layers generally are 0.5 to 2 mm and rarely are more than 3 to 4 mm thick. In one 0.3 m interval 46 major pairs were counted. Some clay layers within the interval were further laminated with fine sand partings only one or two grains thick. Thin-bedded deposits were found at intervals up Canyon Creek to an altitude of more than 520 m, and the cumulative thickness of the deposits may exceed 60 m, suggesting that Canyon Creek was dammed by the Amboy ice for a very long time.

Similar deposits were found at many other places. In an outcrop along the Columbia Tie Road, on the south flank of Dunnigan Mountain, three lenses are interbedded in the till, the largest being 1.5 to 1.8 m thick and 12 to 15 m long.

Boulder trains formed as lag deposits on the floor of outwash channels at several places, including Yacolt basin. East Fork Lewis River contains a large concentration of boulders, especially in the reach downstream from the south end of the Yacolt basin and extending downstream to Lewisville Park. Rock Creek Valley, north of Lewisville Park, was floored with boulders in 1950; since that time most of the boulders have been removed during farming operations.

Boulders, occurring singly and in nests, are widely distributed, with many localities on ridges or hilltops. The boulders range from 0.3 to 3.5 m in diameter and boulders 1.5 to 2.4 m are common.

Erosional Features

Hundreds of low, rounded, elongated hills occur southeastward of Yale Lake. Topographic maps (15-minute Yacolt, and 7½-minute Amboy and Ariel quads.) show that most are elongated in the probable direction of ice movement; west down Lewis River Valley, southwest through Chelatchie Prairie, west along lower Cedar Creek west of Amboy, and southwest from Amboy toward Fargher Lake and Battle Ground.

Local direction of ice movement was controlled by major topographic features; Green Mountain, the uplands east of Chelatchie Prairie, and Yacolt Mountain exercised such local control. The hills are smoothly rounded, soil-mantled, and generally thickly covered with vegetation. A few are cut by roads that expose the till capping and the underlying rock core. In all, till and the underlying volcanic rock was seen on a score or more of these rock drumlins.

Drainage Changes

The most important drainage changes postulated are: 1) pre-glacial East Fork Lewis River flowed northwest through the Yacolt basin to Amboy, and thence down the present course of Cedar Creek to the Lewis River; and 2) pre-glacial Canyon Creek flowed southwest through Chelatchie Prairie to join the pre-glacial East Fork Lewis River at

Amboy. The present drainage and the postulated pre-glacial drainage are shown in Figure 2.

Beginning at the Dole Valley Bridge, East Fork Lewis River has incised a narrow gorge in the broader, pre-glacial valley. The pre-glacial valley floor is well exposed at the south end of the Yacolt basin in Moulton Falls County Park where it is about 0.15 km wide, with drift overlying basalt at an altitude of 183 to 186 m. Post-glacial East Fork Lewis River has cut a narrow gorge about 18 m deep at this point, where it turns from its pre-glacial course to flow westward toward Battle Ground. Figure 3 shows cross-sections of the pre-glacial and post-glacial valleys. Locations of the cross-sections are shown in Figure 2. The floor of the pre-glacial valley is at an altitude of 198 m at the Dole Valley Bridge, and about 185 m at the south end of the Yacolt Basin. It is at an altitude of about 178 m, 35 m below the land surface near the west edge of the Yacolt Basin, as shown by the log of a well for the Town of Yacolt, and probably is 8 or 10 m lower at the center of the basin. Downstream, the altitude of the valley floor was about 114 m at Amboy and 98 m, 2.4 km downstream. For the next 9.65 km, Cedar Creek flows in a broad valley underlain by drift. The gradient in this reach is about 5 m/km. At a point about 4.8 km from its mouth, Cedar Creek cuts through the drift

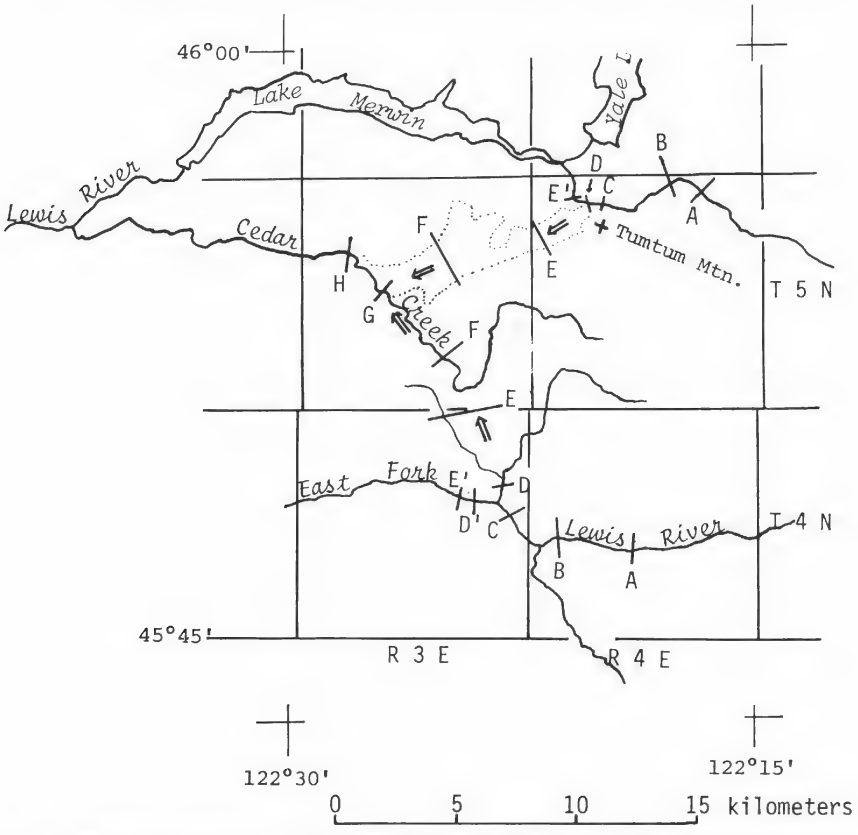

Figure 2. Map showing present and pre-glacial (arrows) drainage, and locations of cross sections.

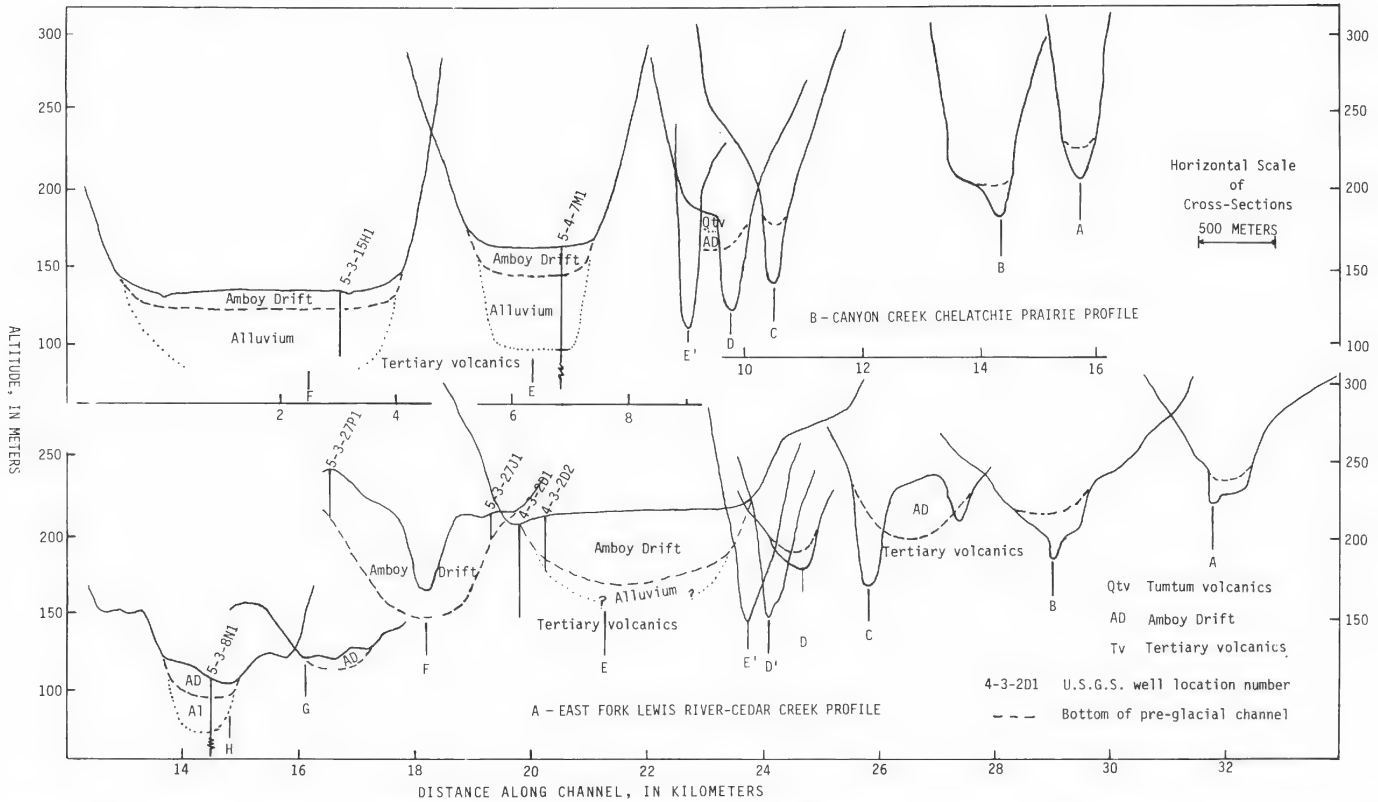

Figure 3. Cross sections and longitudinal profiles along: A—East Fork Lewis River, Yacolt basin and lower Cedar Creek, and B—Canyon Creek and Chelatchie Prairie, showing present profiles and reconstructed pre-glacial profiles. Cross sections have been rotated 90 degrees to plane of profile.

and the pre-glacial valley floor and flows in a canyon sharply incised into basalt. The gradient for the last 4.8 km is nearly 11.4 m/km. The sharply steepening gradient of Cedar Creek near its mouth appears to be further evidence of a change in base level of Lewis River as previously described. The profile of Cedar Creek, and the postulated profile of the pre-glacial East Fork Lewis River, are shown in Figure 4.

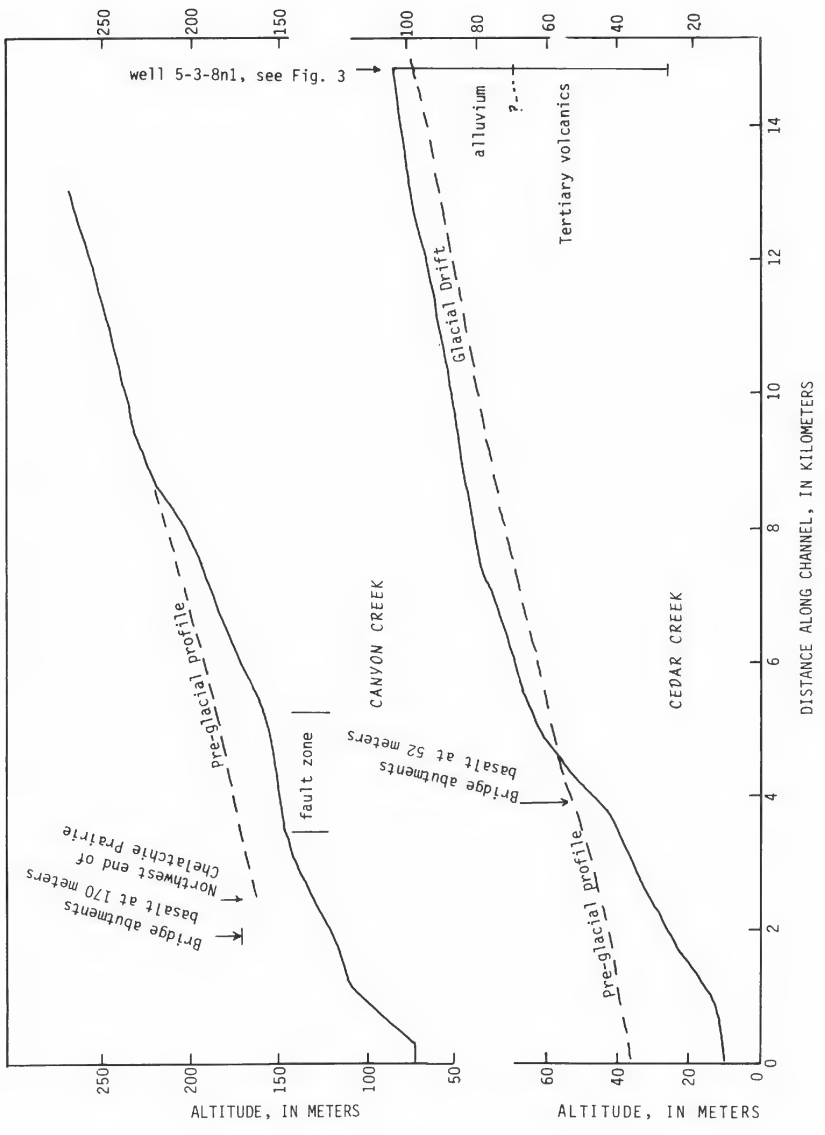

Figure 4. Present profiles, and postulated pre-glacial profiles of the lower reaches of Cedar and Canyon Creeks.

Canyon Creek also has a steeply increasing gradient (see Fig. 4), from a point 8.5 km upstream to its mouth, and the gradient is especially steep for the last 3.2 km. The creek is sharply incised in basalt beginning a km or two northeast of Tumtum Mountain. Both abutments of the bridge across the creek immediately north of the mountain are on basalt of Tertiary age, and till overlies the basalt at an altitude of 170 m. There are no glacial deposits in the downstream reach of the canyon, and it is obvious that this reach is post-glacial. A few hundred meters upstream from this bridge, a flow unit of late Quaternary Tumtum volcanics about 9 m thick overlies approximately 9 m of coarse bouldery Amboy Drift, which in turn overlies Tertiary basalt. The top of the basalt, at an altitude of about 162 m, apparently is the pre-glacial valley floor of Canyon Creek. Canyon Creek followed a course in the down-faulted basin (Mundorff 1964) containing Chelatchie Prairie, to enter the pre-glacial East Fork Lewis River at Amboy. Diversion of Canyon Creek to its present course probably was caused by blockage of its downstream reach by a large mass of ice on Chelatchie Prairie.

Age and Correlation of the Amboy Drift

Depth of weathering and thickness of weathered rinds indicate the relative age of the Amboy glacial deposits. However, the relation between these features and age can be obscured in several ways. At some places part of the surface material appears to have been removed by erosion, resulting in a reduced soil profile. At other places the soil profile has been thickened by soil creep, slope wash, or by deposition of wind-blown deposits. At about 15 outcrops Amboy till was overlain by 0.3 to 1.8 m of yellowish tephra. The tephra at one locality (SW¼ NW¼ sec. 8, T 5 N, R 5 E) was identified by D. R. Crandell (pers. comm.) as Tephra Horizon C from Mount St. Helens (Mulineaux 1978), which is dated as being 35,000 to 40,000 years old. Depth of the oxidized zone, measured at locations where it appeared that there was an undisturbed profile, ranged generally between 1.5 and 2 m, and average depth probably is a little less than 1.8 m. The clayey, less permeable till generally had a thinner profile, whereas sandier, more porous till was oxidized to a greater depth.

Weathering rinds were measured on more than a thousand stones from the upper part of the profile. These stones ranged from pebbles less than 2 cm to boulders more than 1.8 m in diameter. Weathered rinds ranged from less than 0.5 to more than 4 mm thick, but at many localities few or none of the stones had rinds exceeding 2 mm in thickness. It is believed that at most places stones with rinds more than about 2 mm thick are pre-weathered stones that were incorporated into the Amboy Drift from older deposits as the ice advanced over them. In the Fargher Lake-Battle Ground-View area ice overrode the deeply weathered Troutdale Formation. In this area many outcrops contained some pebbles with thick rinds. They also contained some completely rotted pebbles and some quartzite pebbles. The quartzite pebbles and the completely rotted granitic pebbles could have been derived only from the Troutdale, and it seems likely that the other pebbles with thick rinds also were derived from the Troutdale Formation. Pebbles with thick rinds were found side by side with pebbles of similar lithology that had only thin rinds.

The upland east of Amboy is underlain by deeply weathered basaltic and andesitic lavas. In some outcrops spheroidal weathering and exfoliation have produced rounded stones that, after smoothing by the ice, would resemble ice-rounded pebbles and cobbles.

Weathering rinds on 12 such stones ranged from 1.5 to 4 mm and averaged 3.1 mm in thickness. It seems likely that some of the stones with thick rinds, in the till on this upland, are pre-weathered stones derived from the underlying volcanic rock.

During the first part of the field work only the general range and estimated average thicknesses were noted. However, in the last field season individual descriptions were recorded for more than 550 clasts collected at 45 different locations in the Amboy till. Rind thicknesses for these sites, and for 15 sites in the Canyon Creek Drift, are shown in Table 1.

TABLE 1. Thickness of rinds on clasts.

Number of		Percent of rinds within given range (millimeters)							Ave. thickness	
Sites	Clasts	<0.5	0.5-1	1-1.5	1.5-2	2-2.3	3-4	>4	All Rinds	Rinds <2mm
					Amboy Drift					
Amboy-Battle Ground-View Area										
8	108	7.4	25.9	27.8	14.8	10.2	6.5	7.4	1.63	1.08
Yacolt Mountain Area										
2	25	0	32	48	16	4	0	0	1.26	1.17
Upland East of Amboy and Yacolt										
18	221	5.4	33.9	34.4	17.6	4.9	2.7	0.9	1.26	1.10
Lewis River Valley										
7	94	3.2	31.9	50.0	10.6	4.3	0	0	1.17	1.12
Canyon Creek Basin										
9	108	0	32.4	54.6	13.0	0	0	0	1.15	1.15
					Canyon Creek Drift					
15	172	48.3	33.2	15.7	2.3	0.6	0	0	0.60	

In the Amboy-Battle Creek-View area, where the ice overrode the Troutdale Formation, the average rind thickness was 1.63 mm. If the rinds thicker than 2 mm are assumed to be pre-weathered stones, the average thickness is 1.08 mm, about the same as for other areas.

An alternative explanation for the greater rind thickness in the Amboy-Battle Ground-View area would be that some of the outcrops represent an older glacial episode. However, most of the locations where clasts with thick rinds were found are at relatively low altitudes, near the terminus marking the maximum extent of ice. To reach these areas the ice would have had to reach maximum altitudes on the flanks of the Lewis River Valley and on the mountains in the lowland areas, such as Green, Dunnigan, and Yacolt mountains. Scores of outcrops were examined in those localites, and only rarely do the clasts have rinds thicker than 2 mm.

An average thickness of 1.10 to 1.15 mm appears to be a reasonable estimate for the Amboy Drift. This is slightly greater than the 1 mm thickness of rinds from the Hayden Creek Drift in the Mount Rainier region (Crandell and Miller 1974). However, if the percentage of pre-weathered clasts in the Amboy Drift were a bit higher than assumed, the average rind thickness would be nearly the same as for the Hayden Creek Drift.

A large fragment of wood was recovered from the thin-bedded clay along Canyon Creek road. Carbon-14 determination in the University of Washington Quaternary Laboratory showed that the material was older than 60,000 years (QL-1431, Minze Stuiver, pers. comm., 1980). The general appearance and this limiting age determination

suggest that the Amboy Drift is correlative with the Hayden Creek Drift and represents a geological event of early Wisconsin age.

Canyon Creek Drift

In tracing the advance of the Amboy galciation up Canyon Creek valley, it was found that both Amboy-age and a younger drift had originated in the headwaters of the drainage.

Cirques and emphitheaters are found at the head of Canyon Creek and its tributaries. Zig Zag Lake occupies a cirque on the west side of an amphitheatre at the head of Canyon Creek, and Canyon Creek Drift extends downstream to the mouth of Puny Creek, a distance of about 6.4 km. In the Puny Creek Valley, Canyon Creek Drift extends downstream nearly 5 km. In the Pelvy Creek Valley, a terminal morraine of Canyon Creek Drift is a prominent feature south of the center of sec. 5, T 5 N, R 5 E, at an altitude of about 780 m. In Jakes Creek Valley, Canyon Creek Drift extends to within 2 km of its junction with Canyon Creek. At the head of Big Rock Creek, two small streams have cut parallel channels on the east and west flanks of the valley, leaving a narrow ridge of Canyon Creek morraine several hundred meters long in the center of the valley. This morraine is well exposed where Forest Service Road N 525 cuts through the ridge. Canyon Creek Drift extends down valley for about 3.2 km beyond that point, to an altitude of about 490 m.

Canyon Creek Drift also was found along West, Horseshoe, and Calamity Creeks, all tributaries of Siouxon Creek. South of Zig Zag Lake, Canyon Creek Drift was found at the head of the East Fork Lewis River.

Cirque floors, occupied during the Canyon Creek glaciation, range in altitude from about 825 to 915 m. All these drainages trend north, northeast, or northwest, and the lowest cirque floors are in drainages opening directly north. The minimum altitude of about 825 m for the crique at the head of Big Rock Creek is considerably lower than the minimum reported (1000 m) for the Evans Creek glaciation in the Mount Rainier area (Crandell and Miller 1974).

The Canyon Creek till is very cobbly and bouldery, with a gray, sandy, and clayey matrix. At places the pebbles and larger stones are only moderately rounded. Generally, only 0.6 to 0.9 m of soil has developed on the till. The soil is medium to dark brown, grading downward through a yellowish subsoil into gray, unweathered till. Rinds range from less than 0.1 to about 1 mm, and average about 0.6 mm thick. A summary of rind thicknesses is given in Table 1. At some places on occasional stone with a thicker rind is found, probably reworked from older drift or other material. If the few stones with abnormally thick rinds are omitted, the average rind thickness is about 0.5 m.

The average depth of weathering on the Canyon Creek Drift, about 0.75 m, is somewhat greater than the depth on the Vashon till in the Tacoma area, and of the Evans Creek Drift in the Mount Rainier area (Crandell and Miller 1974). Also, according to that report, stones from the Evans Creek Drift generally lack discernable rinds. Rind thickness was measured on about 40 stones collected from the upper part of the soil formed on Vashon till in the Gig Harbor area: rinds ranged up to 1 mm in thickness, 90 percent were less than 0.5 mm, and average thickness was about 0.25 mm. On the basis of rind thickness, the Canyon Creek Drift appears to be older than the Vashon

and the Evans Creek Drifts. However, it is much younger than the Amboy Drift, and probably represents an early event during the Fraser glaciation.

Implications of the Glacial Deposits

The size of the Amboy ice lobe in the lower Lewis River Basin, the great distance it reached in its maximum extent, and the low altitude of its terminus suggest that glaciation was much more extensive on the western flank of the Cascade Mountains in southern Washington than generally recognized. East of the upper end of Swift Reservoir, much of the upland appears to have been glaciated, and most of the drainages heading at 900 m or more must have supported glaciers. The ice lobe in the Lewis River Valey must have been fed by scores of glaciers, and the entire area east of Swift Reservoir may have been covered by an ice cap.

Such extensive glaciation in the Lewis River Basin suggests that extensive glaciation must also have occurred in the Kalama and Toutle River Basins.

Acknowledgements

The helpful suggestions and comments of personnel of the U.S. Geological Survey, especially Bruce Foxworthy, David Dethier, Fred Pessel, D. R. Crandell, and Dee Molenaar, are gratefully acknowledged. Thanks also are extended to Minze Stuiver of the University of Washington for the Carbon-14 determination and to David Matala of the U.S. Forest Service for facilitating entry into the Blue zone south of Mount St. Helens in 1980.

Literature Cited

Crandell, D. R. 1965. The glacial history of Western Washington and Oregon *In* The Quaternary of the United States. Princeton Univ. Press, Princeton, N.J. 341-253.

———, and Miller, R. D. 1974. Quaternary stratigraphy and extent of glaciation in the Mount Rainier region, Washington. U.S. Geological Survey Prof. Paper 847.

———. 1979. Topographic and geologic setting of the Mount St. Helens volcano. Unpublished manuscript.

Hammond, Paul. 1980. Geologic map and cross-section of the Southern Washington Cascade Range. Dept. of Earth Sciences, Portland State Univ., Portland, Oregon.

Hyde, Jack E. 1975. Upper Pleistocene pyroclastic-flow deposits and lahars south of Mount St. Helens volcano, Washington. U.S. Geological Survey Bull 1383-B.

Mundorff, M. J. 1964. Geology and ground-water conditions of Clark County, Washington, with a description of a major alluvial aquifer along the Columbia River. U.S. Geological Survey Water-Suppply Paper 1600.

Received, July 12, 1983
Accepted for Publication, December 30, 1983

W. H. Rickard
and
M. C. McShane
Pacific Northwest Laboratory
P.O. Box 999
Richland, Washington 99352

Demise of Spiny Hopsage Shrubs Following Summer Wildfire: An Authentic Record

Abstract

Spiny hopsage, *Grayia spinosa*, shrubs growing in a plant community dominated by greasewood, *Sarcobatus vermiculatus*, shrubs were destroyed by a summer wildfire. In the first season after the burn, greasewood shrubs sprouted, and by April of the second spring season, greasewood had restored about one-half of its preburn canopy cover. Spiny hopsage shrubs did not sprout and their demise is attributed to stressed growing conditions imposed by an alkaline-sodic rooting substrate. The demise of spiny hopsage would likely have gone unnoticed were it not for the existence of a permanently marked study plot.

Introduction

Wildfires are recurring events in shrubsteppe plant communities growing on the United States Department of Energy's Hanford Site in southeastern Washington. The most abundant shrubs are big sagebrush, *Artemisia tridentata*, and antelope bitterbrush, *Purshia tridentata*. These plants do not sprout after being severely burned. Other taxa; rabbitbrush, *Chrysothamnus nauseosus*, greasewood, *Sarcobatus vermiculatus*, and spiny hopsage, *Grayia spinosa*, are less abundant than sagebrush and bitterbrush but these sprout after burning (Daubenmire 1970). Humphrey (1974) in his extensive review of burning makes no mention of the fire response of spiny hopsage. This article describes the response of spiny hopsage and greasewood, following a summer wildfire, and provides an authentic record of the demise of spiny hopsage by summer burning.

Materials and Methods

The study area is a greasewood-spiny hopsage plant community located on the Arid Lands Ecology (ALE) site on the U.S. Department of Energy's Hanford Site, Benton Co., Washington (Harr and Price 1982). The community lies at an elevation of approximately 250 m above mean sea level. Annual precipitation averages 16 cm. The community has a history of study. Plant-soil-water relationships have been studied by Harr and Price (1972) and Rickard (1967). Sodium and potassium accumulation by greasewood and spiny hopsage leaves has been studied by Rickard (1964, 1965), Rickard and Keough (1968), and Rickard (1982).

The fire history of the community before 1943 is unknown. The community has a known history of heavy livestock grazing between the years 1943 and 1963. In 1963 the community and about 800 acres of surrounding land was fenced to exclude livestock. The community has not since been grazed by livestock, and the riparian woody vegeta-

tion along the nearby spring stream has greatly benefited (Rickard and Cushing 1982).

In 1965 a 30x30 m study plot was staked using 24 steel fence posts spaced at 5 m intervals around the plot perimeter. The only man-induced disturbances since its establishment have been one-day visits to the plot by field ecology classes in April every other year. During these visits seven 30 m lines stretched between opposite fence posts were used to intercept shrub canopies, and the number of living shrubs rooted inside the plot perimeter were counted.

In July 1981, a wildfire burned through the study plot and adjacent areas destroying the aboveground parts of shrubs and the understory herbs. The plot was revisited in April 1983, and canopy-cover and shrub density were determined in the same way as had been done in previous years.

Results

Shrub canopy cover and density determinations made in April 1981 and in April 1983 are summarized in Table 1. The July 1981 wildfire killed 43 spiny hopsage shrubs on

TABLE 1. Canopy cover (percentage) and density of greasewood and spiny hopsage shrubs on a 30x30 m study plot on the Arid Lands Ecology (ALE) Reserve in April 1981 and April 1983.

Shrub Taxa	Number of Shrubs	1) % C	2) % C	Average of 1 and 2
		Preburn Measurements 1981		
Greasewood	185	10.7	12.2	11.4
Spiny hopsage	43	6.4	5.6	6.0
Total	228	17.1	17.8	17.4
		Postburn Measurements 1983		
Greasewood	210	4.8	5.9	5.4
Spiny hopsage	0	0	0	0
Total	210	4.8	5.9	5.4

1) Average of seven east-west lines.

2) Average of seven north-south lines.

the study plot. Greasewood shrubs sprouted vigorously and canopy cover of greasewood was restored to about 47 percent of its preburn values, but only 31 percent of total shrub canopy was restored. There were 185 greasewood shrubs counted on the plot in 1981 and 210 were counted in 1983, an increase of 25 shrubs. Burning apparently stimulated sprounting of greasewood. The dominant herbaceous species in 1981, Sandberg bluegrass, *Poa sandbergii*, and cheatgrass, *Bromus tectorum*, were also the understory dominants in 1983.

Discussion

The community in the past 20 years has supported three shrub species; greasewood, spiny hopsage, and sagebrush. Only a few living sagebrush plants were present in the community 20 years ago, although they were not on the study plot. The dead, standing stems of sagebrush were more numerous than living plants. The absence of charcoal and burn scars on the dead sagebrush stems prior to the 1981 burn indicates that their demise was probably not due to burning. It has been suggested that their demise may have

been initiated by accelerated wind erosion (Rickard 1964). Years of overgrazing and trampling by livestock may have damaged the soil binding understory plants resulting in the loss, by wind action, of several decimeters of surface soil. Loss of top soil could have reduced the soil water holding capacity of a thin soil layer with normal chemistry above a deep alkaline-sodic soil layer, creating a new soil profile unsuited for sagebrush but still acceptable to the more salt-tolerant spiny hopsage and greasewood shrubs.

Our study community differs floristically from other greasewood dominated communities in eastern Washington because salt grass, *Distichlis stricta*, is not a part of the herb understory (Daubenmire 1970). Instead the understory consists of herbs characteristically found in sagebrush dominated communities. The surface soil in the study community was also chemically different from that of greasewood communities elsewhere in Washington. The pH of the surface soil between greasewood shrubs was near neutral, but values of 9 and higher were measured in the surface soil beneath shrub canopies indicating changes in soil chemistry induced by leaf fall and leaf decomposition (Rickard *et al.* 1973). The surface soils between greasewood shrubs in greasewood-saltgrass communities elsewhere in Washington had pH values of 10 (Daubenmire 1970) instead of near neutral as was the case in our community.

Extensive wildfires occurred on the ALE site in the years 1957, 1973, and 1981. However, the study community burned for the first time in 1981, after a 17 year respite from livestock grazing. Cattle grazing tends to suppress the spread of wildfires by keeping the herbaceous biomass (fuel) at reduced levels. The years of protection from grazing has probably contributed to the early demise of spiny hopsage on the study plot by allowing accumulation of herbaceous fuels.

Spiny hopsage is also reported to be very susceptible to the chemical herbicides used to kill weeds in agricultural fields (Daubenmire 1970). Nevertheless, the demise of spiny hopsage in our study community was very likely not caused by fugitive herbicides because the community is remote from agricultural fields and roadside spraying is not practiced.

Spiny hopsage begins its annual growth cycle by putting out new leaves in February. Flowering takes place in March and April and seeds ripen in May and June. Leaves drop from the twigs in summer. This same seasonal pattern of leaf retention and leaf fall has been noted for spiny hopsage growing in southern Nevada (Ackerman *et al.* 1980). Wildfires usually occur on the Hanford Site in July and August when hopsage is aestivating and shrubs are probably least susceptible to fire damage at this stage. Sprouting in the spring is the usual response to summer burning (Daubenmire 1970).

Greasewood shrubs have access to subterranean water via deeply penetrating root systems and the foliage of greasewood shrubs remains green and succulent throughout the hot, dry summer months (Harr and Price 1972). The wetness of the shoots also probably helps to reduce the severity of burn damage and helps to promote a strong sprouting response.

Over the past 17 years sagebrush and spiny hopsage have been lost from the community, indicating that changes in plant species composition can occur for different reasons. It is likely that the demise of spiny hopsage in this community would have gone undetected were it not for the estabishment of the study plot and its data record. The value of permanently marked study plots in detecting changes in plant species composition of natural communities, following unscheduled environmental disturbances,

is demonstrated. The failure of spiny hopsage to sprout after burning suggests that the plants were growing under less than optimal conditions and were therefore sensitive to burn damage in this habitat.

One of the important findings of field research would be to provide some capability to identify plant populations that are "stressed" from those that are "non-stressed." At the present time field indicators of stress are dwarfed plants, chlorotic and necrotic leaves, failure to produce seeds, and other gross morphological features. Research needs to be directed to finding ways to indicate the presence of physiological stress in plant populations that appear to be normal morphologically but react abnormally to man-induced perturbations such as burning, spraying with chemical herbicides, herbivory, or chronic air pollution from industrial facilities.

Acknowledgements

Work performed for the U.S. Department of Energy under Contract DE-AC06-76RL0 1830.

Literature Cited

Ackerman, T. L., E. M. Romney, A. Wallace, and J. E. Kinnear. 1980. Phenology of desert shrubs in southern Nye County, Nevada. Brigham Young University. Great Basin Naturalist Memoirs. Number 4.

Daubenmire, R. 1970. Steppe vegetation of Washington. Wash. Agric. Expt. Sta. Tech. Bull. 62.

Harr, R. D., and K. R. Price. 1972. Evapotranspiration from a greasewood-cheatgrass community. Water Resources Research 8:1199-1203.

Humphrey, R. R. 1974. Fire in the deserts and desert grasslands of North America. *In* Fire and Ecosystems. T. T. Kozlowski and C. E. Ahlgren, eds. Academic Press, New York. Pp. 366-400.

Rickard, W. H. 1964. Demise of sagebrush through soil changes. BioScience 14:43-44.

———. 1965. Sodium and potassium accumulation by greasewood and hopsage leaves. Botanical Gazette 126:116-119.

———. 1967. Seasonal soil moisture patterns in adjacent greasewood and sagebrush stands. Ecology 48:1034-1038.

———. 1982.Cation content of desert shrubs and its relationship to taxonomic and ecological classification. Amer. Midl. Nat. 108:311-316.

———, J. F. Cline, and R. O. Gilbert. 1973. Soil beneath shrub halophytes and its influence upon the growth of cheatgrass. Northw. Sci. 48:96-101.

———, and C. E. Cushing. 1982. Recovery of streamside woody vegetation after exclusion of livestock grazing. J. Range Manage. 35:360-361.

———, and R. F. Keough. 1968. Soil-plant relationships of two steppe desert shrubs. Plant and Soil 29:205-212.

Received, August 25, 1983
Accepted for publication October 15, 1983

David M. Nead

James C. Halfpenny

Mountain Research Station
University of Colorado
Nederland, Colorado 80466

and

Steve Bissell

Colorado Division of Wildlife
6060 Broadway
Denver, Colorado 80216

The Status of Wolverines in Colorado

Abstract

Wolverines (*Gulo gulo*), once classified as furbearers in Colorado, are now afforded complete protection. However, their status in the state is in doubt. This paper reviews historical literature and presents 57 new wolverine reports. Two recent positive reports suggest that wolverines may still exist in Colorado.

Wolverines (*Gulo gulo*) are scarce in the south central Rocky Mountains and reach the southern limits of their distribution in Colorado (Deems and Pursley 1978, Hall 1981, Wilson 1982). Their numbers appear secure in Montana (Newby and McDougal 1964) but in Wyoming they are rare (Hoak *et al.* 1982). Durrant (1952) suggested that wolverines may be extinct in Utah.

Wolverines were once classified as furbearers in Colorado. However, in 1965 the season was closed and wolverines were afforded complete protection. The Colorado Wildlife Commission classified the wolverine as an endangered species in 1973. This paper reviews historical literature and presents 57 new wolverine reports for the state of Colorado. These reports were gathered through a Colorado Division of Wildlife (DOW) project.

Wilson (1982) suggested that wolverine numbers are increasing in Colorado. However, there never has been a population estimate on which to base such a suggestion and it is doubtful that wolverines were ever common in Colorado. Elliot Coues (1879) stated "it is only of late years that the presence of this remarkable animal so far south has been known." Historical records were often based on sight observations (Armstrong 1972, Cary 1911, Field and Feltner 1974, Spahn 1954, Warren 1942). A total of 22 reports, representing at least 25 animals, were based on wolverine carcasses between 1871 and 1919. The last verified kill of a wolverine in Colorado occurred in 1919 (Grinnell 1926). Quick (1964) stated that the occurrence of wolverines in Colorado "in modern times is doubtful."

The Colorado Division of Wildlife initiated a wolverine project in 1978 to summarize the history of wolverines in Colorado and to accumulate information about current wolverine status. Historical information was sought by searches of museum material and

through a review of published literature. Unpublished records were inspected. Historical and current information were also sought by statewide "information request" campaigns. These campaigns employed slide programs, newspaper articles, and distribution of over 3,000 "wanted" posters to district wildlife managers, taxidermists, trappers, outfitters, private individuals, and state and federal agencies. A report form was developed to standardize the evaluation of wolverine sightings. This form was sent to all individuals reporting a wolverine encounter.

Study areas were selected based on returned reports. Snowmachines and skis were used to search these areas for either wolverine or their signs. Baited hair snags, consisting of hardware cloth cylinders with barbed wire interiors, were set to obtain hair samples. Reference slides of hair were prepared from collections at the Denver Museum of Natural History and the University of Colorado Museum. Three keys proved particularly helpful in identifying hair samples taken from snags (Brown 1942, Mayer 1952, Moore *et al.* 1974).

A total of 265 reports of wolverine observations were evaluated during the study. Reports were rated as follows: positive reports, 3; probable reports, 18; possible reports, 36; and non-wolverine reports, 208. The 57 reports classified as positive, probable, and possible are mapped in Figure 1. A detailed listing of reports is available from the authors.

Some of these observations deserve special mention:

1 Three wolverines have escaped from Cheyenne Mountain Zoo in Colorado Springs (Fig. 1, no. 1). A female, which escaped in 1964, was killed by Terry Schmidt on West Las Vegas Street. A second female, which escaped in 1966, was killed by Ray Goecher of Littleton, Colorado in the Rampart Range on February 18, 1966 but the escaped male was never found. These reports were counted as one positive report.

2) July 1977, Al Williams, Assistant Principal of Delta High School, Delta, Colorado found a wolverine skull on the East Fork of the Cimmaron drainage (Gunnison County) (Fig. 1, No. 2). This skull was probably less than ten years old. This report was counted as positive.

3) June 1978, George Lanum of Denver took three photographs of an animal crossing a snow field on Trinchera Peak (Fig. 1, no. 30). His description and the body shape in the photograph suggest a wolverine.

4) June 1978, Mr. and Mrs. Robert Haas of Texas photographed one adult and three young animals west of Lake City (Fig. 1, no 9). The animals were too distant for positive identification. However, the drawings and descriptions made by the Haas's indicate wolverines.

5) October 1978, Stouffer Productions, Aspen, Colorado released two wolverines while filming a movie. The wolverines, which were imported from Canada, were released east of Castle Peak, Pitkin County (not mapped). Three reports in the general vicinity since their release may relate to these animals.

6) March 1979, Robert Kay of Vernal, Utah shot a male wolverine allegedly three km west of the Colorado-Utah border on U.S. Highway 40 (Fig. 1, no. 3). There is reason to doubt that the animal came from Utah. Also, since wolverines may roam over 32 km per day, if this animal came from Utah he probaby had part of his range in Colorado.

7) March 1979, Don Roberts, Gary Guggenberger, and Ron St. Pierre of the Colorado Division of Wildlife watched an animal for three minutes at 25 m near the Rifle

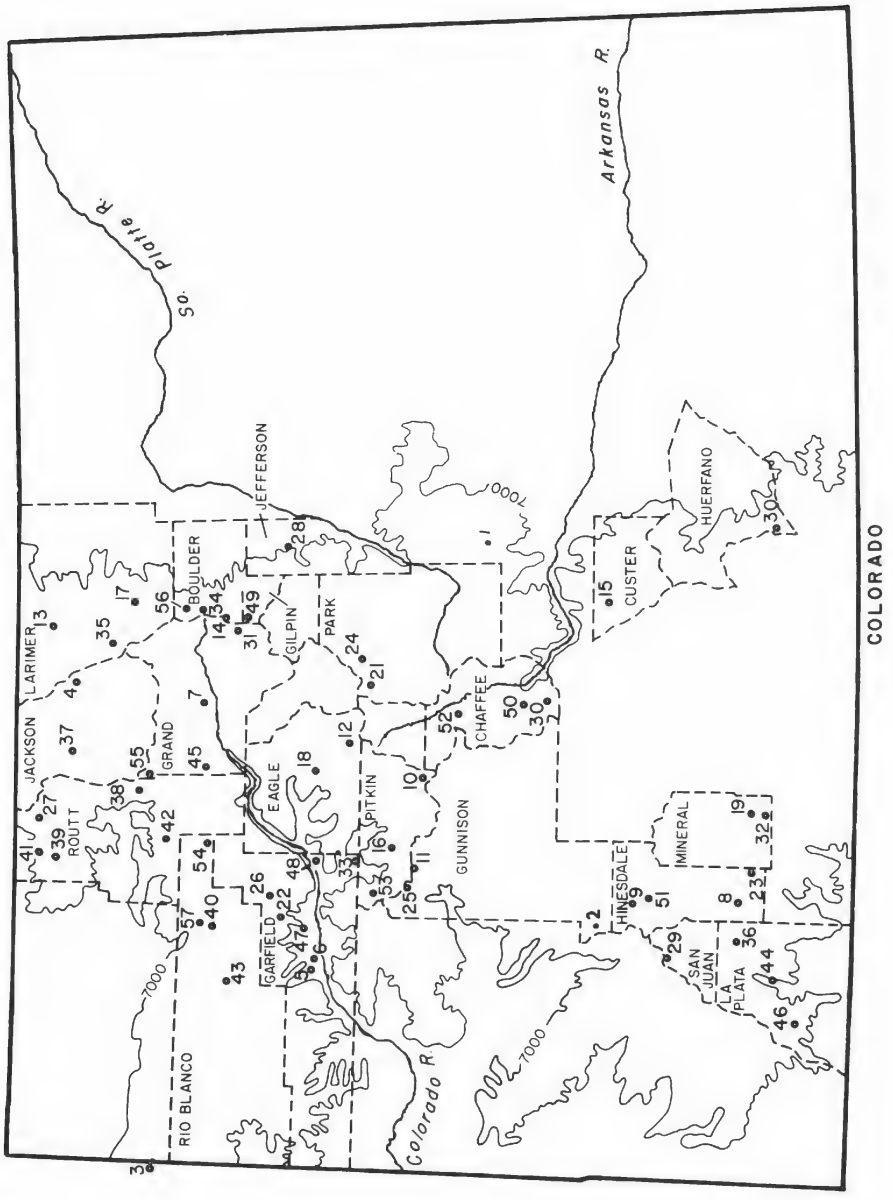

Figure 1. Distribution of 57 wolverine reports in Colorado. Counties are shown only if reports occurred within the county. The 7000 ft contour is also indicated.

Colorado Fish Hatchery (Fig. 1, no. 5). They identified the mammal as a wolverine and the sighting was in an area of other credible reports.

8) June 1979, Kurt Keskamaki watched an animal as it approached a bear bait that he had set near Parshall, Colorado (Fig. 1, no. 7). He watched the animal at less than 10 m for four minutes. Description, behavior, and signs indicated a wolverine.

Despite several credible reports the study did not verify the presence of viable populations of wolverine in Colorado. Verified wolverine include one skull found, one wolverine killed allegedly 3 km west of Colorado-Utah border, and two wolverines killed near Colorado Springs. In addition, two wolverines were imported and released by private interests. Repetition in credible reports suggests areas where wolverine are still likely to be found in Colorado. These include the San Juan Mountains (north of Durango and southeast of Wolf Creek Pass) and the southwestern portion of the Flat Tops Wilderness (Garfield County). North and west of Rocky Mountain National Park is another possibility.

We believe wolverines continue to exist in Colorado. However, irrefutable proof of viable populations is absent due to difficulty in detection and obtaining positive proof. Even if positive proof of a wolverine were obtained, it would not prove the existence of a viable population.

We wish to thank the numerous volunteers and DOW personnel who helped on this project, in particular, Dr. David Armstrong (CU), and Gary Miller (DOW). This paper is a contribution to Colorado DOW Federal Aid Endangered Species Project SE-3-2.

Literature Cited

Armstrong, D. M. 1972. Distribution of mammals in Colorado. Monogr., Univ. Kansas Mus. Nat. Hist. 3:x+1-415.

Brown, F. M. 1942. The microscopy of mammalian hairs for the anthropologists. Amer. Phil. Soc., Philadelphia. Proc. 85:250-274.

Cary, M. 1911. A biological survey of Colorado. N. Amer. Fauna. 33:1-256.

Coues, E. 1879. Notice of Mrs. Maxwell's exhibit of Colorado Mammals. Pp. 217-225. *In* On the plains and among the peaks: or how Mrs. Maxwell made her natural history collection (Dartt-Thompson, M. A.). Claxton, Remsen, and Haffelfinger, Philadelphia.

Deems, E. F., Jr., and D. Pursley. 1978. North American Furbearers: Their Management, Research, and Harvest Status in 1976. Int. Assoc. Fish Wildl. Agencies. Univ. of Maryland, College Park, Maryland.

Durrant, S. D. 1952. Mammals of Utah. Univ. of Kansas Publ., Mus. Nat. Hist. 6:1-426.

Field, R. J., and G. Feltner. 1974. Wolverine. Colorado Outdoors 23:1-6.

Grinnell, G. B. 1926. Some habits of the wolverine. J. Mamm. 7:30-34.

Hall, E. R. 1981. Mammals of North America. John Wiley and Sons, New York.

Hoak, J. H., J. L. Weaver, and T. W. Clark. 1982. Wolverines in western Wyoming. Northw. Sci. 56:159-161.

Mayer, W. V. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. Amer. Midl. Nat. 48:480-512.

Moore, T. D., L. T. Spence, and C. E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department Bull. 14:1-177.

Newby, F. E., and J. J. McDougal. 1964. Range extension of the wolverine in Montana. J. Mamm. 36:485-487.

Quick, H. F. 1964. *In* Rodeck, H. G. Natural History of the Boulder Area. Univ. Colorado Mus.

Spahn, J. J. 1954. Wolverine. Colorado Cons. 3:1-3.

Warren, E. R. 1942. The Mammals of Colorado. Univ. Oklahoma Press.

Wilson, D. E. 1982. Wolverine (*Gulo gulo*). Pp. 644-652 *In* J. A. Chapman and G. A. Feldhamer, eds. Wild Mammals of North America: Biology, Management, and Economics. Johns Hopkins Press, Baltimore.

Received, March 9, 1983
Accepted for publication, June 14, 1983

Kevin R. Moore

and

Charles J. Henny

U.S. Fish and Wildlife Service
Patuxent Wildlife Research Center
480 SW Airport Road
Corvallis, Oregon 97333

Age-specific Productivity and Nest Site Characteristics of Cooper's Hawks (Accipiter cooperii)

Abstract

Nesting Cooper's Hawks (*Accipiter cooperii*) were studied in northeastern Oregon. Second-year (SY) males did not breed, but 22 percent of the breeding females were SY's. Mean clutch size ($P = 0.012$) and mean number of young fledged per pair that laid eggs ($P < 0.10$) were lower for SY females than for adult (after second year [ASY]) females; however, an equal percentage of the eggs (excluding a collected sample egg) yielded fledged young for each age class. Stepwise discriminant analysis suggested differences in structural characteristics of the nest site habitat for ASY and SY females, i.e., SY female nest sites were associated with younger successional stages than ASY female nest sites. Nests of both age groups were built in trees with high crown volume, but ASY females utilized mistletoe (*Arceuthobium* sp.) for nest structures more frequently ($P < 0.01$) than SY females.

Introduction

Age of breeding individuals affects many aspects of reproductive performance of several bird species including raptors. Nesting habitat use, mate selection, laying date, clutch size, and breeding success can be affected by age and experience (Coulson and White 1958, Greenwood *et al.* 1979, Middleton 1979, Newton 1979). Individuals breeding for the first time seem to have lowered reproductive success. Younger breeding females generally lay smaller clutches and raise fewer offspring than older individuals.

Most raptors do not begin breeding in juvenal plumage and require varying periods of time to acquire adult plumage. Breeding of raptors in juvenal plumage may be evidence of favorable breeding conditions or higher numbers of unoccupied territories (Newton 1979). Henny *et al.* (1973) found a breeding SY female Red-shouldered Hawk (*Buteo lineatus*) nesting successfully when the overall breeding density was lowest on a study area in central Maryland. Cooper's Hawks (*Accipiter cooperii*) retain juvenal plumage for one year and generally do not breed the first year (Reynolds and Wight 1978). The present study examines productivity and nest site characteristics of breeding ASY and SY Cooper's Hawks in northeastern Oregon.

Study Area and Methods

Study Area

The study area was located within and around Wallowa-Whitman National Forest of northeastern Oregon between 45° and 46° North Latitude at elevations between 500 m and 1600 m. The Wallowa-Whitman National Forest is in the Blue Mountains province

of Oregon and consists primarily of montane forest with moderate to steep relief. A detailed description of the physiognomy of this province and climatic conditions of the various forest types are given by Franklin and Dyrness (1973). Hall (1973) recognized several climax forest plant communities in this area: ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), grand fir (*Abies grandis*), subalpine fire(*A. lasiocarpa*), and mixed conifer stands, e.g., ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), grand fir, and western larch (*Larix occidentalis*). Many stands are on a gradient between these community types. Vegetation on natural open areas consists of grass and forb species. A mosaic of forest stands of various age classes and species composition is present in the region.

Vegetation Sampling

Nests at undisturbed sites which had been located between 1975 and 1979 were sampled in 1978 and 1979. Vegetation was sampled within 0.08 ha circular plots centered at the nest tree. Vertical distribution of tree crown volume was measured by the technique of Mawson *et al.* (1976) and the program HTVOL. Each tree within the plot was considered in relation to 15 possible crown shapes and relegated to the one it fitted best. The dimensions of these shapes were measured using a clinometer and a steel tape. The HTVOL program calculated total crown volume within 3 m height classes up to 30 m to develop a crown profile for each plot. Diameter at breast height (DBH) and species were recorded for each tree in the plot. All plants greater than 0.3 m and less than 3 m tall were measured as shrubs. Shrub crown volume was calculated by fitting shrubs or groups of shrubs into the smallest possible cube and measuring the dimensions of that cube. Shrub and tree crown volumes were combined to develop a total crown profile for each plot.

The following nest tree characteristics were recorded: species, condition (alive, dead), DBH, and crown height. The following nest characteristics were measured: height, nest substrate, and canopy coverage at the nest (measured with a spherical densiometer).

Productivity

Clutch size and number of bandable young (3-4 weeks old) were recorded. When possible, one egg was removed from each nest for analysis of pesticide contamination. Productivity for each age group was determined by using only nests at which clutch size and number of 3-4 week old young were known and where an egg was removed from the clutch.

Age Determination

Breeding individuals were trapped and banded at nest sites just before or immediately after fledging of the young. Age was determined by differences in plumage. Birds were placed into two age classes: SY birds were one year old and retained juvenal plumage, and ASY birds were two years or older with adult plumage. Initial molting of juvenal plumage and replacement by darker adult plumage were evident during the incubation period and continued through the breeding season.

Analysis

Tree crown profiles and stand composition variables at nest sites were tested for differences between age groups by using multivariate techniques. A stepwise discriminant analysis was used to select those variables most important in discriminating between nest sites of each age group. A canonical analysis on nest site variables was used to identify those variables which were the most powerful discriminators of each age group's nest site characteristics (Morrison 1967).

We tested differences in clutch size and numbers of young fledged among years using a Kruskall-Wallis one-way ANOVA. We tested differences in clutch size, number of young fledged, and fledging success between age groups using a Wilcoxon rank sum test (Conover 1971). Computer analyses utilized the Statistical Analysis System (SAS; Helwig and Councils 1979) and the Statistical Package for the Social Sciences (SPSS; Nie *et al.* 1975).

Results

Age and Productivity

Forty-five occupied Cooper's Hawk nests were observed. Of the 37 breeding females which were aged, 8 (22 percent) were in SY plumage. The percentage of the breeding population consisting of SY females is much higher than the previously reported 6 percent by Reynolds and Wight (1978) and Meng (1951), but similar to the 20 percent reported by Hennessy (1978). Henny and Wight (1972) inferred that 30-37 percent of the Cooper's Hawk population in the eastern United States consisted of SY's during the breeding season. Assuming a similar proportion for our study area, the observed 22 percent SY breeding females suggests that perhaps about half of the SY females were nesting. Only 15 of 45 breeding males were aged but all were in adult plumage. The absence of breeding SY males was also observed by Reynolds and Wight (1978) in Oregon and Meng (1951) in New York. In 1979, one SY male was caught foraging within 50 m of a nest, but it was not known if this was the male of that breeding pair.

There were no differences among years in mean clutch size ($P > 0.44$) or for mean number of young fledged per pair that laid eggs ($P > 0.83$). Therefore, productivity data were combined from the four years to examine age differences.

Mean clutch size for SY females was significantly lower than mean clutch size for ASY females ($P = 0.012$, Table 1). ASY females laid a higher proportion of four or five egg clutches whereas most SY female clutches had three or four eggs. As expected, mean number of young fledged per pair that laid eggs was also lower for SY females ($P < 0.10$). The percentage of eggs laid (after one egg removed) that yielded fledged young (fledging success) was comparable for both age groups ($P > 0.38$,

TABLE 1. Comparison of clutch size in SY and ASY female Cooper's Hawks.

Female age	N	Nests by clutch size					Clutch size[1]
		1	2	3	4	5	$\bar{x} \pm SD$
SY	8	0	1	4	3	0	3.25 ± 0.70
ASY	20	0	0	3	10	7	4.20 ± 0.69

[1]Before egg removal.

Table 2). However, the systematic removal of an egg from each nest probably increased fledging success of remaining eggs for both age classes, e.g., 19 successful ASY female nests (with one egg removed) fledged an average of 2.63 (82 percent of remaining eggs) whereas 8 successful ASY female nests (with no eggs removed) fledged an average of 3.00 (71 percent of eggs laid).

The percentage of nest attempts successful in fledging at least one young was slightly higher for ASY females than SY females (Table 2); however, the unadjusted estimates are biased high because most nests were not found on the day of clutch initiation (Steenhof and Kochert 1982). Nests that failed early could be missed, especially when nests were located by sign (prey remains) and adult activity which increased as the nesting season progressed. The percentage of nests successful was indeed lower for each age class when based on the Mayfield Exposure Day method (for details see Steenhof and Kochert 1982), but age class values were not statistically different ($P > 0.05$).

Overall, after an adjustment for the sample egg collected (assuming 71 percent of eggs in successful nests yielded fledglings) and the undetected loss of nests (based on Mayfield's approach), we estimated that 2.64 young were fledged per ASY female that laid eggs, and 1.73 young per SY female. Newton et al. (1981) reported SY European Sparrowhawks (*Accipiter nisus*) also laid smaller clutches (4.20) than older females (4.60) and fledged fewer young per nesting attempt (1.55 [SY] vs. 2.27 [third year] or 2.35 [older] famales).

TABLE 2. Comparison of productivity between SY and ASY female Cooper's Hawks (nests with a sample egg collected).

Female age	N	Young fledged $\bar{x} \pm SD$	Fledging success[1] $\bar{x} \pm SD$	Percent nests successful[2]
SY	8	1.75 ± 1.0	0.78 ± 0.37	87.5 (75.0)
ASY	20	2.50 ± 1.1	0.78 ± 0.30	95.0 (88.1)

[1]$\bar{x}$ young fledged/$\bar{x}$ clutch size - 1.

[2]Unadjusted data, ( ) adjusted by Mayfield Exposure Day method as detailed in Steenhof and Kochert (1982), with 61 day exposure period.

Age and Nest Site Characteristics

Crown profiles from mean crown volume values were developed for each age group (Fig. 1). Nest sites of SY females had greater crown volumes from 0 to 6 m, but smaller crown volumes from 12 to 21 m than did sites of ASY females; volumes for other strata were similar for each age group. This indicates a greater proportion of small trees or shrubs in nest sites of SY females. This trend in vegetative structure is further illustrated by the frequencies of trees in various size classes (Table 3). SY females nested in stands of younger successional stages or stands which had undergone recent selective overstory removal. Vegetative structure of nest sites used by SY females more closely resembled those nest sites used by Sharp-shinned Hawks (*Accipiter striatus*) which also utilize stands of early successional growth stages (Moore and Henny 1983).

Crown volume in the ten 3-m strata, frequency of each tree size class, basal area, and stem density were used in a stepwise discriminant analysis to test for differences between age groups in vegetative structure of nest sites. The stepwise discriminant identified those variables most important in discriminating between groups in a step-

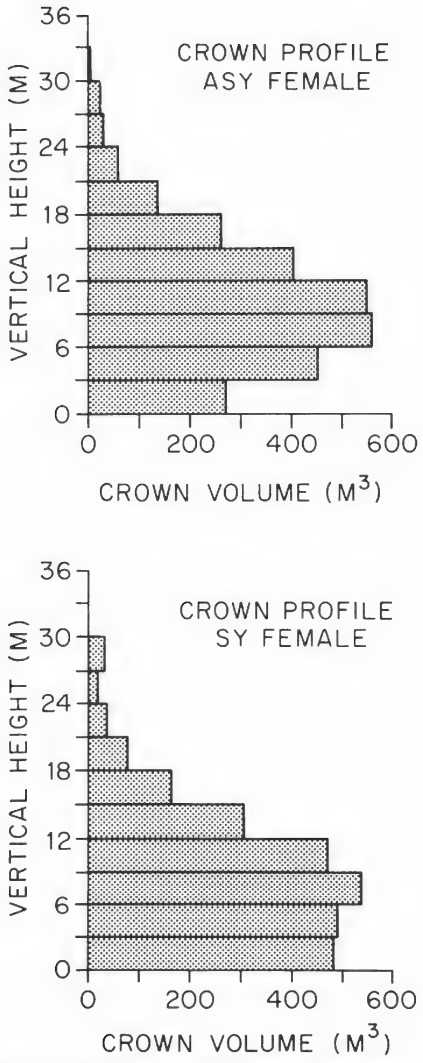

Figure 1. Crown profiles at nest sites of SY and ASY female Cooper's Hawks.

wise fashion. The discriminant function developed from this procedure then provides a means of classifying the original observations by using *a posteriori* probabilities of group membership. Nest sites of SY females were correctly classified for seven of eight observations, suggesting that structural differences existed in nest sites used by each age group (Table 4).

Age-specific separation of nest site habitat can be graphically represented by using canonical analysis of the habitat variables. Canonical analysis generates new variables which are linear combinations of the original variables, each weighted according to their power to discriminate the groups (Morrison 1967). The position of individual observa-

TABLE 3. Structural characteristics at nest sites of SY and ASY female Cooper's Hawks.

Variables	SY females $\bar{x} \pm SD$		ASY females $\bar{x} \pm SD$	
Tree size class (cm DBH)				
2.5- 8.9	90.4	95.8	79.4	63.3
8.9-16.5	49.4	25.5	40.4	22.2
16.5-31.7	21.4	10.4	26.7	12.0
31.7-41.9	4.7	2.7	6.3	4.7
> 42	1.7	1.9	2.4	3.7
Stems/0.08 ha	158.6	112.0	155.3	78.9
Basal area M^2	2.6	0.8	3.2	1.4
Mean DBH cm	13.7	5.0	14.2	5.3

TABLE 4. Classification results from the discriminant analysis of nest site variables of SY and ASY females.

Group	N	SY females	ASY females
SY females	8	7	1
		87.5%	12.5%
ASY females	25	4	21
		16.0%	84.0%
Unknown age	6	2	4
		33.3%	66.7%

tions can be plotted along the canonical functions to get a graphical interpretation of the nature and extent of group separation. Variables and their associated standardized coefficients, selected by stepwise discriminant analysis were used to specify the canonical functions. Habitat separation of nest sites between age groups is graphically displayed in Figure 2. Some nest sites were used by both ASY and SY females which increased

TABLE 5. Nest tree characteristics for SY and ASY female Cooper's Hawks.

Variables	SY females $\bar{x} \pm SD$		ASY females $\bar{x} \pm SD$	
DBH[1] (cm)	36.3	13.7	40.9	16.2
Nest height[2] (m)	10.7	3.4	12.4	2.8
Nest-crown relationship[3] (m)	3.4	3.4	1.7	5.5
Canopy coverage[4] (%)	96.2	3.4	94.7	5.7
Frequency of mistletoe use as nest structure[5]	50.0%		70.0%	

[1]$Z = 0.65$, $P > 0.50$; [2]$Z = 1.28$, $P > 0.20$; [3]$Z = 0.80$, $P > 0.40$; [4]$Z = 1.00$, $P > 0.32$; [5]$Z = 5.50$, $P < 0.01$.

overlap along the canonical axis.

Age and Nest Tree Characteristics

SY females appear to place nests lower in height than ASY females, but higher in the crown of the nest tree (nest-crown relationship, Table 5). Sites for both age classes have similar nest canopy coverage. None of these variables were significantly different between age groups (Wilcoxon rank sum test). Comparison of nest tree characteristics and crown profiles (Fig. 1) reveals a trend for each age group to build nests in strata with high crown volumes. The frequency of mistletoe use as a nest structure was significantly lower for SY females ($P < 0.01$). Mistletoe growth provides a nest building

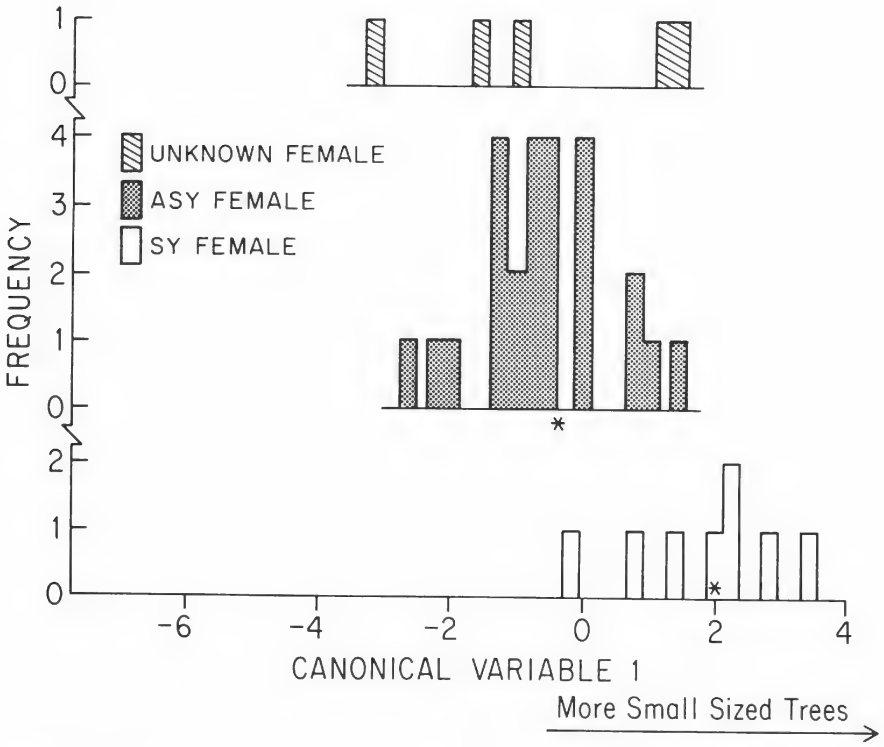

Figure 2. Distribution of observations at nest sites of SY and ASY females along the canonical axes. *Represents group means.

structure that effectively conceals nests from researchers, and possibly predators, searching from the ground. But, the percentage of nests on mistletoe that were successful (96 percent) was not significantly higher ($P > 0.28$) than for nests not on mistletoe (86 percent).

Discussion

The lower productivity of SY females may result from (1) behavioral and physiological differences associated with age, (2) habitat differences (including prey availability) where they nest, or (3) a combination of the above.

Smaller clutch sizes associated with juvenal plumaged females has been demonstrated in several species of birds including raptors (Hickey and Anderson 1969, Perrins and Moss 1974, Harvey *et al.* 1979, Newton *et al.* 1981). Charnov and Krebs (1974) predicted optimal clutch sizes to be smaller than the most productive clutch size due to the relationship between adult survival and clutch size. Energy expenditure by parents increases with brood size causing weight loss and lowered survivorship in adults (Klomp 1970, Cody 1971). This factor would be more important to longer-lived birds such as raptors which may breed several times in a lifetime. If younger birds are less experienced in foraging ability and therefore less efficient at feeding themselves and their

young, then smaller clutch sizes would reduce food stress and increase survival allowing individuals to breed in subsequent years.

Given the smaller clutch size for SY females in our study, we showed an equal percentage of the eggs yielding fledged young for each age group. Our study, however, was confounded by the removal of an egg from each clutch for pesticide analysis. Removal of an egg, assuming it would hatch, lowered brood size and probably increased survival of the remaining siblings. However, once eggs are laid and incubation has begun, the males take the major responsibility of capturing prey for the female and the young up to about two weeks post hatch.

Vegetative structure differences at nest sites are suggested between age groups. The "quality" of the nest site and its effect on productivity is difficult to determine. Nest sites provide concealment and inaccessibility from predators and shelter for young from adverse weather. Nest sites probably vary in the ability to provide these factors and raptors may respond to these differences. This response may be altered by experience and younger, less-experienced, individuals may select lower quality nest sites. Nest failure during our study occurred at nests of SY and ASY females but all occurred at sites which were used by a SY female at some time during the study. A nest site occupied by an ASY female was unsuccessful in 1976; it was occupied the following year by a SY female and failed again. The same site was used the following year by another SY female and all the young were preyed on by a Great Horned Owl (*Bubo virginianus*). The site was used by three different males during those three years. The vegetative structure at this nest site may have been inadequate for concealment from predators. Possibly the concealment factor or the presence of Great Horned Owls in the vicinity precluded the use of the site by most adult females.

Success or failure of a season's reproductive effort may be important in the learning process of selecting a good nest site. However, the territory surrounding the nest site is also important. Newton (1979; Table 42) found that female European Sparrowhawks nesting in "good," "intermediate," and "poor" habitats (based on food availability) returned the following year to nest sites in good habitat more often than to nest sites in poor habitat. Also, within a given habitat category, females returned to the same territory significantly more often after a successful nest attempt than after a failure. Unfortunately, we made no assessment of food availability during the study, but 10 (59 percent) of 17 nest sites were reused the following year by an adult female. At least 3 of the sites (18 percent) were used by the same female. No sites were reused by adult females after unsuccessful nest attempts, and no SY females returned to nest sites used the previous year whether successful or not.

In this study, the proportion of SY female Cooper Hawks in the breeding population was the highest reported for the species. Newton (1976) found the greatest number of SY European Sparrowhawks breeding in the most productive habitats, which he attributed to high population turnover from shooting or the occurrence of favorable conditions necessary to induce yearlings to breed. Middleton (1979) found that breeding first-year American Goldfinches (*Carduelis tristis*) in Ontario using optimal habitat had a greater chance of nesting success than in lower quality habitats. However, studies of other passerine species indicate that young birds are often displaced into suboptimal habitat by older members of the population (Brown 1969, Krebs 1972). Henny *et al.* (1973) found that adult Red-shouldered Hawks used flood plain areas for nesting in

central Maryland but non-breeding SY's were restricted to upland areas away from prime nesting habitat.

If SY females nest in suboptimal territories, then some differential mate selection by females may be operating and differences in male quality may be inferred. Banding data indicate that this population is migratory (Henny, unpublished banding data), therefore, nesting territories are established each spring. Mate selection may be occurring on the basis of territory quality or characteristics of the male such as age, breeding experience, or quality of nuptial feeding. Territory quality was most important in female choice of Red-winged Blackbird (*Agelaius phoeniceus*) mates, and male genetic quality was next in importance (Searcy 1979). Burley and Moran (1979) indicated that feral Pigeons (*Columbia livia*) showed a preference for mating with individuals with greater breeding experience and age, but individuals older than seven years were not selected as mates. Newton (1979) found that choice of mates in European Sparrowhawks was selective by age, young birds pairing and older birds pairing. The greater probability of nesting success with more experienced individuals in a breeding pair confers selective advantage to older birds in this type of pairing. Eye color darkens with age in both male and female Cooper's Hawks (Snyder and Snyder 1974). Age-related changes in eye color may convey information about the age of the individual which influences mate selection. If preferential pairing of Cooper's Hawks occurs based on these criteria, then SY females could be displaced into suboptimal habitats and forced to breed with less experienced males. Under these circumstances, the smaller clutch size of SY females may be advantageous.

In summary, we have demonstrated differences in clutch size and suggested differences in nest site habitat (more habitat data is needed) for SY and ASY female Cooper's Hawks. The role of age (behavioral and physiological) vs. habitat is an intriguing subject for future ecological research.

Acknowledgments

Many individuals and agencies cooperated in this study. Nest sites were located by a number of U.S. Fish and Wildlife Service employees, including Roger Olson and Tracy Fleming, who worked on the project for several field seasons. Laurel Rubin assisted in collecting the habitat data. The Oregon Department of Fish and Wildlife and the U.S. Forest Service provided living quarters during a portion of the study. Jack Thomas, Director of the Range and Wildlife Habitat Laboratory of the U.S. Forest Service, provided office space and a number of ideas about designing the study. Ralph Anderson, Tom Thomas, and other U.S. Forest Service employees provided information on *Accipiters* nesting in the study area. Karen Steenhof's computer program was used to estimate nesting success. Barry Noon and Mark Fuller kindly reviewed an early draft. The U.S. Forest Service partially funded this study with a contract to the U.S. Fish and Wildlife Service.

Literature Cited

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81:293-329.

Burley, N., and N. Moran. 1979. The significance of age and reproductive experience in the mate preference of feral Pigeons, *Columba livia*, Anim. Behav. 27: 686-698.

Charnov, E. L., and J. R. Krebs. 1974. On clutch size and fitness. Ibis 116:217-219.

Cody, M. L. 1971. Ecological aspects of reproduction. *In* D. S. Farner and J. R. King, eds. Avian Biology, Vol. I. Academic Press, New York, N.Y.

Conover, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons, New York, N.Y.
Coulson, J. C., and E. White. 1958. The effect of age on the breeding biology of the Kittiwake, *Rissa tridactyla.* Ibis 100:40-51.
Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. Dept. Agric. For. Serv. Gen. Tech. Rep. PNW-8.
Greenwood, P. J., P. H. Harvey, and C. M. Perrins. 1979. Mate selection in the Great Tit *Parus major* in relation to age, status and natal dispersal. Ornis Fennica 56:75-86.
Hall, F. C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. U.S. Dept. Agri. For. Serv. R6 Area guide 3-1.
Harvey, P. H., P. J. Greenwood, C. M. Perrins, and A. R. Martin. 1979. Breeding success of Great Tits *Parus major* in relation to age of male and female parent. Ibis 121:216-219.
Helwig, E. S., and K .A .Councils, editors. 1979. SAS users guide, 1979 edition. SAS Institute, Inc., Raleigh, North Carolina.
Hennessy, S. P. 1978. Ecological relationships of *Accipiters* in northern Utah—with special emphasis on the effects of human disturbance. Utah State Univ., Logan. M.S. Thesis.
Henny, C. J., and H. M. Wight. 1972. Population ecology and environmental pollution: Red-tailed and Cooper's Hawks. Pages 229-250 *in* Population ecology of migratory birds: a symposium. U.S. Fish and Wildl. Serv. Wildl. Res. Rep. No. 2.
———, F. C. Schmid, E. M. Martin, and L. L. Hood. 1973. Territorial behavior, pesticides, and the population ecology of Red-Shouldered Hawks in central Maryland, 1943-1971. Ecology 54:545-554.
Hickey, J. J., and D. W. Anderson. 1969. The Peregrine Falcon: life history and population literature. *In* J. J. Hickey, ed. Peregrine Falcon Populations, Their Biology and Decline. Univ. of Wisc. Press, Madison, Wasconsin.
Klomp, H. 1970. The determination of clutch-size in birds. A review. Ardea 58:1-124.
Krebs, J. R. 1971. Territory and breeding density in the Great Tit *Parus major* L. Ecology 52:2-22.
Mawson, J. C., J. W. Thomas, and R. M. DeGraff. 1976. Program HTVOL the determination of tree crown volume by layers. U.S. Dept. Agri. For. Serv. Res. Paper NE-354.
Meng, H. K. 1951. The Cooper's Hawk *Accipiter cooperii* (Bonaparte). Cornell Univ., Ithaca, N.Y., Ph.D. thesis.
Middleton, A. L. A. 1979. Influence of age and habitat on reproduction by the American Goldfinch. Ecology 60:418-432.
Moore, K. R., and C. J. Henny. 1983. Nest site characteristincs of three coexisting Accipiter hawks in northeastern Oregon. Raptor Res. 17:65-76.
Morrison, D. F. 1967. Multivariate Statistical Methods. McGraw-Hill Publishing Co., New York, N.Y.
Newton, I. 1976. Breeding of Sparrowhawks (*Accipiter nisus*) in different environments. J. Anim. Ecol. 45:831-849.
———, M. Marquiss, and D. Moss. 1981. Age and breeding in sparrowhawks. J. Anim, Ecol. 50:839-853.
———. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, South Dakota.
Nie, N., C. H. Hull, J. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical Package for the Social Sciences. McGraw-Hill Publishing Co., New York, N.Y.
Perrins, C. M., and D. Moss. 1974. Survival of young Great Tits in relation to age of female parent. Ibis 116:220-224.
Reynolds, R .T., and H. M. Wight. 1978. Distribution, density, and productivity of Accipiter hawks breeding in Oregon. Wilson Bull. 90:182-196.
Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to Red-winged Blackbirds (*Agelaius phoeniceus*). Am. Nat. 114:77-100.
Snyder, N. F. R., and H. A. Snyder. 1974. Function of eye coloration in North American Accipiters. Condor 76:219-222.
Steenhof, K., and M. N. Kochert. 1982. An evaluation of methods used to estimate raptor nesting success. J. Wildl. Manage. 46:885-893.

Received March 16, 1983
Accepted for publication, July 7, 1983

Timothy D. Reynolds[1]

Biology Department
Idaho State University
Pocatello, Idaho 83209

Daily Summer Movements, Activity Patterns, and Home Range of Pronghorn

Abstract

Daily movements, activity patterns, and spatial and behavioral use of summer home ranges of pronghorn (*Antilocapra americana*) were examined by radiotelemetry in southeastern Idaho from June through August 1980. Five pronghorn were located every 30 minutes over 16 24-hour sampling periods. Daily movements for bucks and does averaged ($\bar{x} \pm$ SD) 15.9 $\pm$ 4.4 and 20.4 $\pm$ 8.1 km, respectively. The size and shape of summer home ranges were estimated by the minimum area method and two grid-size analyses. Some areas within each home range were used exclusively for resting or loafing, while others were used only for feeding. Two major (0430 - 0630 and 1930 - 2230 MST) and 2 minor (0930 - 1130 and 1330 - 1630 MST) peaks of feeding activity occurred daily. Pronghorns spent approximately 30 percent of each day feeding and 65 percent resting or loafing. Rapid directional movements accounted for about 5 percent of the daily activity. With the possible exception of one, none of the study animals moved to and used open water during any of the 24-hour sampling periods.

Introduction

The advantages and shortcomings of radiotelemetry systems and methodologies in monitoring wildlife by remote sensing have been well documented (Slater 1963, Heezen and Tester 1967, Biggins and Pitcher 1978, Amlaner and Macdonald 1980, and others). With some notable exceptions (Mech 1967, Knowlton *et al.* 1968, Woodruff 1977, Laundré and Keller 1981), wildlife studies involving radiotelemetry were generally designed to determine an animals area of use (home range: Burt 1943) and/or document migration routes and distances traveled. Although these studies provided reliable data on the spatial use of the environment, they had only limited ecological application (Sanderson 1966, Laundré and Keller 1981). They failed to provide much useful information on how habitat was being used, *viz.* the animal's activity or behavioral use. This was an acute problem if the study animals could not be observed visually, or, as in the case of pronghorns, the animals were often alert to the observer and hence modified their activity. Recently biologists have increased the amount of information gained via telemetry by locating the animals more frequently (Rongstad and Tester 1969, Woodruff 1977, Laudré and Keller 1981). When telemetric locations of an animal were determined at hourly intervals or less, behavioral use could then be estimated by analyzing the movement and velocity patterns. Using this approach, the objective was to study the daily activity patterns and area of use of selected pronghorns on the Idaho National Engineering Laboratory (INEL) in southeastern Idaho.

---

[1]Present Address: Radiological and Environmental Sciences Laboratory, U.S. Department of Energy, 550 Second Street, Idaho Falls, Idaho 83901.

Methods

The INEL occupies 2,315 km^2 of semiarid, cold-desert rangeland on the Snake River Plain approximately 48 km west of Idaho Falls, Bonneville County, Idaho. Atwood (1970), Nace *et al.* (1972, 1975), Harniss and West (1973), McBride *et al.* (1978), and Anderson and Holte (1981) provide detailed descriptions of the climate, geology, and vegetation of the INEL. In general, the topography is flat to gently rolling, with frequent lava outcroppings characteristic of the Columbia Plateau Province. The vegetation of the site is dominated by big sagebrush (*Artemisia tridentata*). During the study, ambient temperatures ranged from 1.7 to 31.1°C. Average daily minimum and maximum temperatures were 6.1 $\pm$ 2.7° and 26.8 $\pm$ 3.7° C, respectively. Total precipitation from June-August 1980 was 4.9 cm. For the period two days prior to and including each 24-hour sampling regime, rainfall in excess of 0.2 cm was recorded only four times. Trace amounts of rainfall for the same interval preceding and including the the remaining sampling dates occurred five times.

During late April 1979, Idaho Department of Fish and Game personnel and researchers from the INEL Environmental Sciences Branch placed solar-powered radiotransmitters (Wildlife Materials, Carbondale, IL) on 15 pronghorn (Autenrieth *et al.* 1981). Five of these animals (two bucks, three does) were the subject of this study from June through August 1980. All animals, except a two-year old male, were adults at least three years of age. Neither of the bucks was territorial.

Initial plans were to locate each animal every 30 minutes during five separate 24-hour sampling periods spaced at 2-3 week intervals during the summer. Animals were monitored from a four-wheel drive vehicle with a portable, programmable receiver (Cedar Creek, Bethel, MN) equipped with a null-peak junction box. Twin five-element yagi antennas were mounted on a rotating mast that extended into the cab of the vehicle.

For each location two compass readings were taken and the animal's position was estimated by triangulation. The general procedure was to take a compass bearing from a known point, quickly drive to a second point (generally 0.8 km away) and take another reading. This process was repeated every 30 minutes until 49 pairs of readings were recorded. Heezen and Tester (1967) reported that the position of an animal obtained by triangulation rarely represented its actual location. They stated that the degree of error depended upon the accuracy of each compass reading, the angle of the intersection of the bearing lines for each pair of fixes, and the distance from the animal to the monitoring device. During this study, the distance from the vehicle to the animal rarely exceeded 1 km, and generally was from 0.5 to 1.0 km. Efforts were made to take compass readings from points at which the bearing lines would intersect at the optimum 90° to reduce the error polygon.

Triangulation error was determined by taking 10 pairs of compass readings on a stationary transmitter from distances ranging from 0.5 to 1.5 km. In no trial was the calculated position greater than 100 m from the actual location of the transmitter. Because a time lapse of 2-6 minutes occurred between the first and second compass readings for each pair of fixes, the distance between the true and calculated location of an animal increased if the animal was moving. This displacement error was estimated by taking compass readings on a transmitter carried in a vehicle on a known path at speeds up to 15 km/hour. Only at the greatest velocities was the location error more than 250 m, with most calculated locations being less than 150 m from the actual

locations. The above tests for triangulation error indicated that the calculated location of the animal was most likely within 200 m of its true position.

Patterns of spatial use (home range) during the summer were determined by computer analysis using the grid method described by Rongstad and Tester (1969), Fossey (1974), and Caro (1976). When using this technique, the reliability of the estimate of the home range size depends on the number of new grids entered by an animal during each successive sampling period. The number of new grids entered is, in turn, a function of the grid size. Theoretically, when large grids are used, the number of new grids entered during each additional sampling period rapidly approaches zero. But, this results in the inclusion of areas within the grids that are not actually used by the animal. When extremely small grids are used, the probability of including non-use areas is minimized, but new grid use does not decline significantly with each successive sample. Grid sizes of 1.0 (1 x 1 km) and 0.25 km^2 (0.5 x 0.5 km) were examined for suitability of estimating pronghorn home ranges. Results based on these grid sizes were compared with the more conventional minimum area method of estimating home range size described by Mohr (1947), Stickel (1954) and Mohr and Stumpf (1966).

Distances between successive locations were determined by computer analysis (Laundré 1979) and the rate of travel (velocity) was calculated and recorded as distance (km) per hour. All distances between successive locations were assumed to result from straight line movement at a constant rate of travel. A frequency distribution, augmented by field observations, was used to classify velocities into behavioral categories and to study 24-hour activity patterns.

Velocities of different behaviors, to be used as standards for determining the behavioral use of home ranges, were ascertained by observing free-ranging pronghorn. An animal's position was marked on a detailed map of the area and its activity subjectively classified as resting (recumbent)/loafing (upright and stationary), feeding, or rapid directional movement. When the activity obviously changed to another behavioral category, the time expired was noted and the new position (if any) was recorded. Using these data, calculating velocities for each behavioral category was possible.

Velocities for each 30-minute interval for the 24-hour sampling periods were calculated by dividing the distances between successive locations by the time between fixes (30 min). These data were grouped into 0.2 km/hr intervals and a frequency distribution was generated. This distribution was examined and compared with data from field observations to assess the usefulness of the velocities assigned to each category of behavior. When the velocity for each activity was thus identified, the frequency of occurrence of each type of activity was plotted against time of day to illustrate daily activity patterns.

Once the appropriate grid size for estimating home range size was selected and the velocities of each movement type were determined, the behavioral use of each home range was examined. To do this, the velocity at which an animal moved during each 30-minute interval was recorded for each grid the subject animal entered during that particular time period. These velocities were compared to the previously determined rate of travel for each activity class, and each grid in every home range was then classified according to behavioral use. Unless stated otherwise, all mean values are $\bar{x} \pm SD$.

Results

Because of transmitter failures and other difficulties, only 18 of 25 planned 24-hour studies were completed. Data from two of these were excluded from analysis because monitoring activities disturbed the subject animals and obviously influenced their movements and behavior. The results are therefore based on 16 successful 24-hour samples. The 2-year-old buck was monitored during two complete 24-hour cycles. Two does were each tracked for three complete cycles, and the remaining buck and doe were each followed for four 24-hour periods.

Home Range: Spatial and Temporal Use

As expected, the number of new 1.0 km^2-grids entered by each pronghorn during successive 24-hour sampling periods quickly declined (Fig. 1A). Initially, the number of

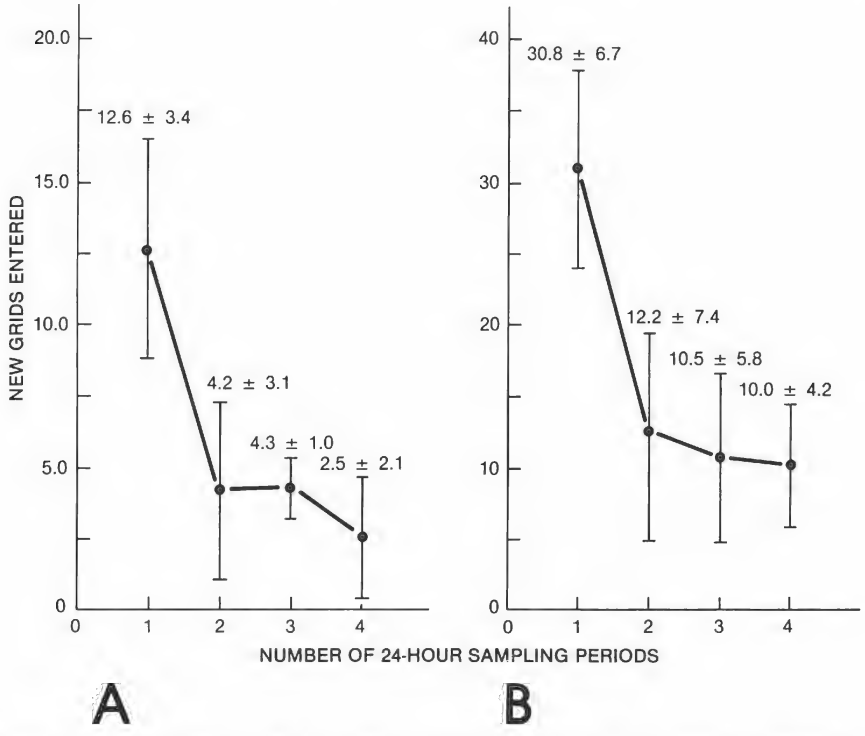

Figure 1. Number of new 1.0 km^2 (A) and 0.25 km^2 (B) grids ($\bar{x} \pm$ SD) entered by pronghorn in successive sampling periods on the INEL Site, June-August 1980. Note: ordinate scale values differ.

new 0.25 km^2-grids entered also sharply declined, but after the second sampling period (Fig. 1B), this leveled off to about 10 new grids entered during each successive sampling period. Home range size estimates did not differ significantly ($P > 0.20$; t-test) between the 0.25 km^2-grid analysis and the minimum area method (Table 1.). Estimates of home range size were significantly larger ($P < 0.05$) when calculated using the

TABLE 1. Estimates of 1980 summer home ranges (km^2) of pronghorn on the Idaho National Engineering Laboratory Site determined by 1.0 and .025 km^2-grid analyses and the minimum area method.

			Estimated home range (km^2)		
			Grid Method		Minimum Area
Sex	Animal	N	1.0 km^2	0.25 km^2	Method
Female	527	3	26	17.75	14.87
Female	509	4	22	15.52	12.82
Female	616	3	17	11.00	9.52
Male	704	2	24	14.00	12.24
Male	738	4	17	11.00	10.20
All Females[a]	10		21.67 ± 4.51	14.76 ± 3.44	12.40 ± 2.70
All Males[a]	6		20.50 ± 4.95	12.50 ± 2.12	11.22 ± 1.44
All animals[a]	16		21.20 ± 4.09	13.85 ± 2.93	11.93 ± 2.14

[a]Total home range estimates reported as $\bar{x} \pm SD$.

larger grid size. Although the results varied among methods by as much as 95 percent, the average home range for males and females did not differ ($P > 0.40$; t-test) regardless of which method of measurement was used.

Data from Female 527 were used to illustrate the size and shape of the home range

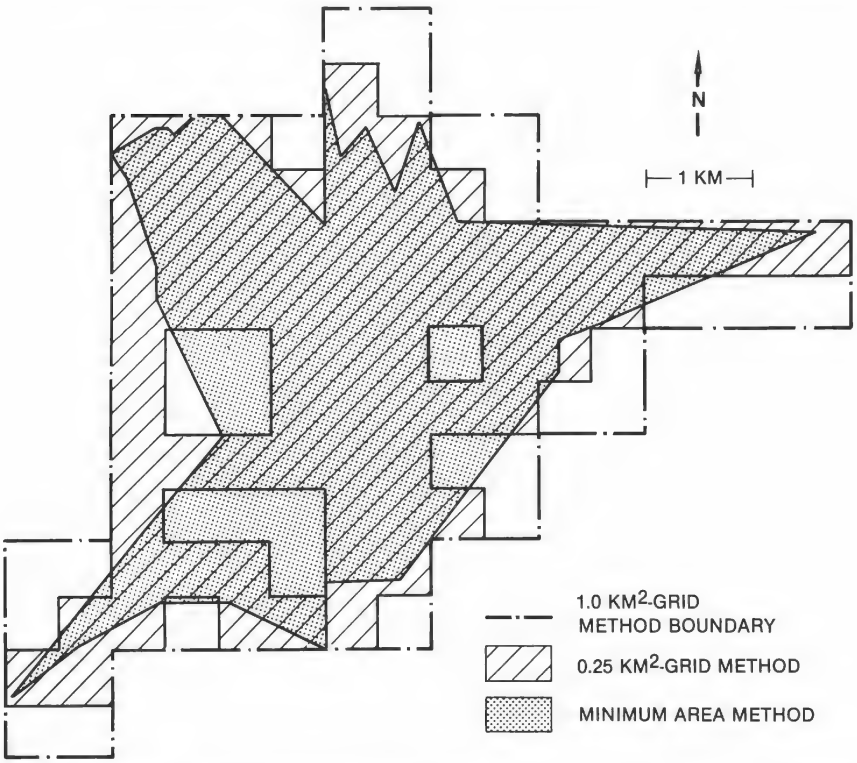

Figure 2. Home range determined by 3 methods for Female 527 on the INEL Site, June-August 1980.

as measured by the different grid size analyses and the minimum area method (Fig. 2). The latter method and the 1.0 km^2-grid analysis both included areas within the home range boundaries that were not recordede as areas of use when the 0.25^2-grid system was employed.

For consistency, data from Female 527 were used again to illustrate the time spent in each 0.25 km^2-home range grid cell (Fig.. 3). Home range use was not uniform. An

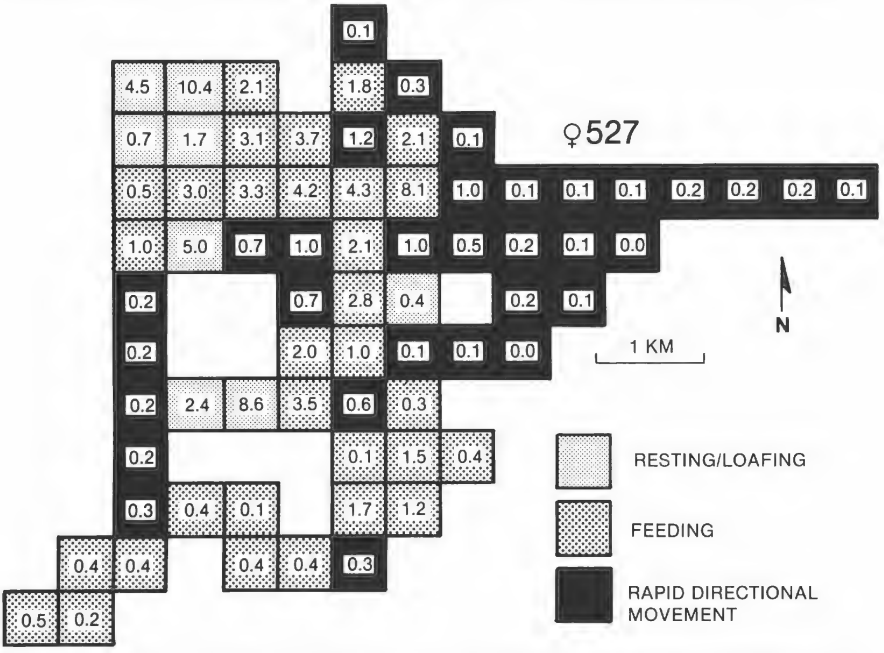

Figure 3. Activity and percent of the total time spent by Female 527 in each 0.25 km^2-grid cell of her home range on the INEL Site, June-August 1980. Values rounded to the nearest 0.1 percent.

area of intensive use occurred roughly in the northwest portion of her home range. Following Craighead *et al.* (1973), this area was called the center of activity and included all grid cells occupied by the doe at least 2 percent of the total monitoring time. Thus, while the center of activity comprised only 25 percent of the total home range area, the doe occupied the activity center more than 75 percent of the time. For all five study animals, the centers of activity composed 17-29 percent of each home range and averaged about 3.5 km^2. Animals were within their centers of activity 65-80 percent of the time.

Home Range: Behavioral Use

Data from Female 527 indicated that the behavioral use of each estimated home range was not uniform (Fig. 3). That is, some grid cells within the home range were used only for resting/loafing, while others were used exclusively for feeding or rapid directional movement. With few exceptions, cells that were used during more than one sampling period or more than once during a single sampling period, were used for the

same purpose. While rapid directional movement tended to occur at the outer edges of the home range, this behavior was also occasionally recorded within the center of activity. Conversely, although resting/loafing and feeding behavior were the predominant behavioral classes recorded in the activity centers, these behaviors were not restricted to those areas and were recorded throughout the home range.

Behavioral Categories and Daily Activity Pattern

A priori, three main categories of pronghorn behavior were selected: resting/loafing, feeding, and rapid directional movement. Field observations indicated that during resting, pronghorn would occasionally rise from recumbency, move a short distance, and again lie down. The distance of these movements was generally less than 100 m at a velocity of less than 0.6 km/hr. Similarly, loafing animals periodically changed their location.

Feeding behavior was observed and defined as a prolonged slow walk associated with browsing activity. Feeding velocities ranged from 0.8 to 1.8 km/hour. Rapid directional movement ranged from a fast walk to a full run and velocities of 2.0 to 51.4 km/hour were calculated from field observation data. Maximum velocities were usually a short burst of speed associated with disturbance (predators, vehicles, intraspecific interaction). Only rarely did pronghorn cover more than 0.5 km at the maximum velocity.

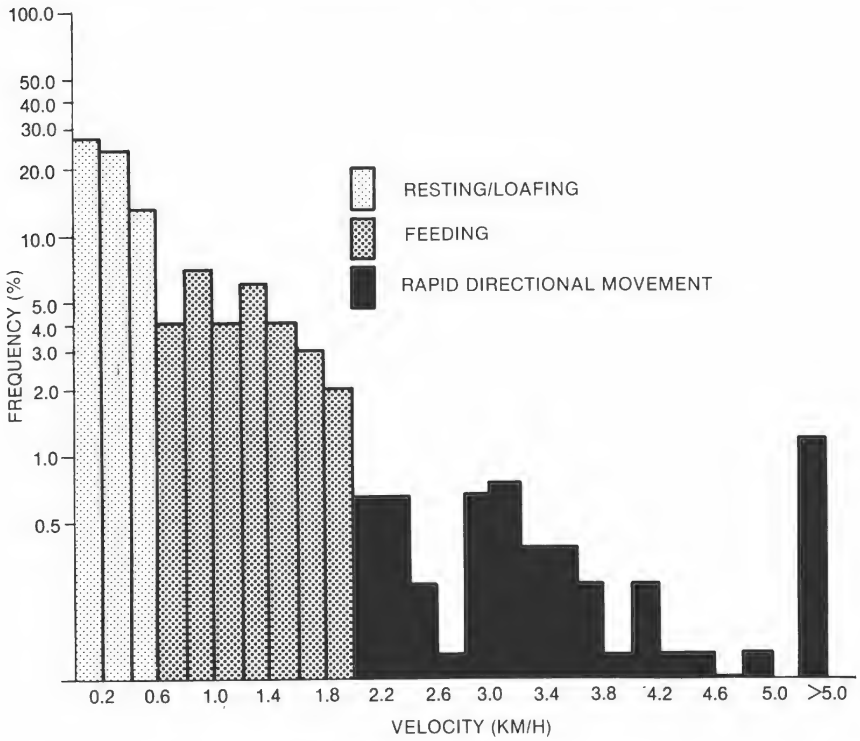

Figure 4. Frequency distribution of velocities recorded via radiotelemetry for pronghorn on the INEL Site, June-August 1980. Data for each 0.2 km/hour interval are presented as a percent of the total number of 30 minute intervals (768) between radio-fixes.

When velocities recorded from the 24-hour samples were grouped into 0.2 km/hour intervals, the resultant percent frequency distribution (Fig. 4) indicated that the frequency of the rates of movement for each behavioral class were different. This suggested that the velocity groupings (< 0.6, 0.6-1.8, and > 1.8 km/hour) from field observations could be identified via radiotelemetry and would provide a reliable classification of velocities into behavioral categories.

A frequency distribution of the time of occurrence for each type of behavior indicated the daily pattern of pronghorn activity (Fig. 5). Daily movements for bucks and

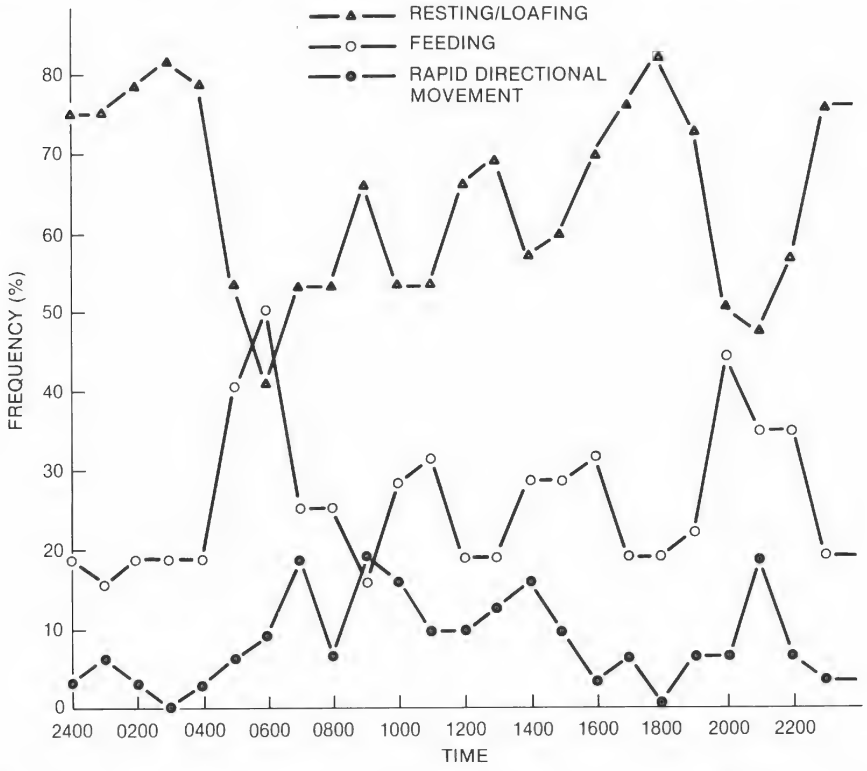

Figure 5. Daily activity patterns of pronghorn on the INEL Site, June-August 1980. Data points for each behavioral use are presented as a percent of the total possible number of movements (32) recorded on the hour and the following half-hour telemetry readings.

does average 15.9 $\pm$ 4.4 and 20.4 $\pm$ 8.1 km, respectively. These were not significantly different ($P > 0.20$) and the average daily movement for all pronghorn sampled was 18.5 $\pm$ 7.1 km per day.

Discussion

During this study, all three does with transmitters were in summering groups consisting mostly of does and fawns, an occasional yearling buck, and usually a territorial male. The radio-collared 2-year-old buck was a member of a bachelor band of 6-8 males. Animals within each group tended to move as a unit, and although the precise loca-

tions of each animal varied, the movement and habitat use by each radiomarked animal was considered to be representative of the group. The one mature buck in this study was a solitary, non-territorial animal, blind in one eye and perhaps beyond reproductive age.

Home range estimates based on the 1.0 km^2-grid analysis ranged from 67 to 96 percent ($\bar{x} = 78$ percent) larger than those calculated by the minimum area method (Table 1). Estimates based on this grid size included areas within the home range that were not delimited by either of the other methods (Fig. 2). Use of a 1.0 km^2-grid size was thus considered inappropriate for accurately estimating size of pronghorn home ranges. When a 0.25 km^2-grid size was used to estimate home range, the results averaged 16 percent (range: 8-21 percent) larger, but not significantly different from those calculated by the minimum area method (Table 1). The 0.25^2-grid analysis also delineated travel corridors between successive locations that were not shown by the minimum area method (Fig. 2), and defined some non-use areas within the boundary of each home range. Thus, the 0.25^2-grid analysis was considered a sensitive and accurate method of estimating pronghorn home range size and was used for subsequent temporal, spatial and behavioral analyses of home range use.

The average summer home range from the 0.25 km^2-grid analysis was 13.85 ± 2.95 km^2. This was 17 percent larger than the average 11.5 km^2 winter home range for adult does determined (minimum area method) by Bayless (1969) in Montana, and considerably smaller than the 20.33 ± 3.22 km^2 ($N = 34$) average summer home range (minimum area method) reported by Hoskinson and Tester (1980) in southeastern Idaho. The latter study included home range estimates for yearlings which the investigators reported as having summer ranges 2-5 larger than adults. Eliminating their yearling home ranges resulted in an average summer home range for adult pronghorn of 13.65 km^2 ($N = 25$), similar to the findings of this study.

Pronghorn used specific areas within their home range for different behavioral activities (Fig. 3). The majority of the behaviors recorded within the centers of activity were resting/loafing and feeding. This was consistant with the findings of Craighead *et al.* (1973) for elk (*Cervus elaphus*) in Yellowstone National Park, where nearly 85 percent of all feeding and bedding occurred within the centers of activity.

Pronghorn exhibited two major and two minor peaks of feeding activity daily. Major peaks occurred early in the morning (0430-0630 MST) and in the late evening (1930-2230 MST) (Fig. 5). Kitchen (1974) and Amstrup (1978) also reported morning and evening peaks in feeding activity. I additionally recorded minor periods of feeding activity during mid-mornings and mid-afternoons. Overall, feeding accounted for nearly 30 percent of the daily activity. This is below the 50-60 percent frequency of feeding recorded by Amstrup (1978) during dawn, daylight, and dusk hours. These differences are probably the result of differences in monitoring techniques and/or habitat quality. Bouts of feeding were generally separated by periods of resting/loafing, although rapid directional movement increased following the major morning and during the major evening feeding periods. Apparently the marked pronghorn, and presumably others, began each day by feeding near their overnight resting areas. They then moved away to ruminate, and spent the daylight hours alternately feeding and resting/loafing. About 65 percent of each day was spent resting/loafing (Fig. 4). This percentage is considerably higher than that reported by Beuchner (1950) and

Amstrup (1978) who found pronghorn inactive less than 30 percent of the time. Differences in periods of inactivity reflect the differences in foraging activity given above. During or after a major late-evening feeding bout, pronghorn moved to an area for overnight resting. These areas changed little from night to night, and without exception were within the center of activity of the home range. Pronghorn generally rested during the night when coyotes (*Canis latrans*), the main predator of pronghorn resident on the INEL, were most active (Lanudre' and Keller 1981). Nightly selection of the same resting areas may afford pronghorns increased security resulting either from familiarity with the area or from the presence of some undetermined topographic or physiogomic feature of the area.

Total daily summer movements in excess of 15 km were not uncommon for pronghorns. Yoakum (1978) reported that summer movements ranged from 0.1 to 0.8 km. His data probably represents the linear distance between the two most distant points that animals moved during the course of a day, rather than the total distance actually traveled. The minimum and maxmium linear distances pronghorn moved in a day in this study were 2.3 and 8.0 km ($\bar{x} = 4.5$ km). These data correspond more closely with the daily range from fall and winter movements of 3.2-9.7 km reported by Yoakum (1978). Differences in daily movements between his summer data and those from this study are most likely the result of different sampling procedures and study areas.

Open water was known to be within the boundary of only one of the five home ranges defined in this study. Thus, while one radio-collared animal and her band had access to free water and possibly drank daily, no evidence indicated that the other four study animals and their bands did so. Published reports of water use and requirements for pronghorn are conflicting. In reviewing this topic, Prenzlow (1965) cited references indicating water use by pronghorn varied from drinking each morning and evening (Kautz 1942) to water demands being met by the production of metabolic water (Davis 1960). Yoakum (1978) and Amstrup (1978) suggested that pronghorn go to water daily and imply that pronghorn avoid areas where free water is not available. Einarsen (1948) reported that pronghorn drink water if it is available, and if it is not, the moisture content in the vegetation consumed meets daily water needs. Phelps (1978) maintained that in Arizona, Sonoran pronghorn (*A. a. sonoriensis*) may go from May to August without drinking water. Directional movements to a water source were not recorded during this study. This tentatively implies that the study animals and the bands they were with relied on the moisture in the vegetation to provide sufficient water for metabolic maintenance during the study period.

Acknowledgments

This paper is a contribution from the INEL Ecological Studies Program, supported by the Office of Health and Envrionmental Research, U.S. Department of Energy, with a grant to F. L. Rose, Idaho State University and with additional funds from Idaho Federal Aid to Wildlife Restoration Project W-160-R. R. E. Authenrieth and G. L. Copeland of the Idaho Department of Fish and Game provided valuable assistance in radio-collaring the pronghorn. I thank J. Grant, J. Bronough, T. Day, and especially K. Grover for their enthusiasm and credible field efforts. I also thank J. W. Laundre' for his suggestions, discussions, and assistance in the computer analyses. R. E. Autenrieth, F. L. Rose, J. W. Laundre', M. W. Barrett, E. Ficher, O. D. Markham, C. E. Braun and

two anonymous referees reviewed drafts of the manuscript. I am grateful for their contributions.

Literature Cited

Amlaner, C. J., and D. W. MacDonald. 1980. A Handbook on Biotelemetry and Radio Tracking. Proc. Int. Conf. Telemetry and Radio Tracking in Biology and Medicine. Pergamon Press, New York, N. Y.

Amstrup, S. C. 1978. Activities and habitat use patterns of pronghorns on Montana-Wyoming coal lands. Proc. Bien. Pronghorn Antelope Workshop. 8:270-304.

Anderson, J. E., and K. E. Holte. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. J. Range Manage. 34:25-29.

Atwood, N. D. 1970. Flora of the National Reactor Testing Station. Brigham Young Univ. Sci. Bull. Bio. Ser. Vol. II, 4.

Autenrieth, R. E., G. L. Copeland, and T. D. Reynolds. 1981. Capturing pronghorn using a helicopter and etorphine hydrochloride. Wildl. Soc. Bull. 9:314-319.

Bayless, S. R. 1969. Winter food habits, range use, and home range of antelope in Montana. J. Wildl. Manage. 33:538-551.

Biggins, D. E., and E. J. Pitcher. 1978. Comparative efficiencies of telemetry and visual techniques for studying ungulates, grouse, and raptors on energy development lands in southeastern Montana. PECORA IV Symp. on Application of Remote Sensing Data to Wildlife Management. Sioux Falls, South Dakota.

Buechner, H. K. 1950. Life history, ecology, and range use of the pronghorn antelope in Trans-Pecos, Texas. Am. Midl. Nat. 43:257-354.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24: 346-352.

Caro, T. M. 1976. Observations on the ranging behavior and daily activity of lone silverback mountain gorillas (*Gorilla gorilla beringei*). Anim. Behav. 24: 889-897.

Craighead, J. J., F. C. Craighead, Jr., R. L. Ruff, and B. W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison drainage herd as determined by biotelemetry. Wildl. Monogr. 33.

Davis, W. E. 1960. The Mammals of Texas. Texas Game and Fish Comm. Bull. 41.

Einarsen, A. S. 1948. The Pronghorn Antelope and its Management. Wildl. Manage. Inst., Washington, D.C.

Fossey, D. 1974. Observations on the home range of one group of mountain gorillas (*Gorilla gorilla beringei*). Anim. Behav. 22:568-581.

Harniss, R O., and N. F. West. 1973. Vegetation patterns of the Idaho National Reactor Testing Station, Southeastern Idaho. Northw. Sci. 47:30-43.

Heezen, K. L., and J. R. Tester. 1967. Evaluation of radio-tracking by triangulation with special reference to deer movements. J. Wildl. Manage. 31: 124-141.

Hoskinson, R. L., and J. R. Tester. 1980. Migration behavior of pronghorn in southeastern Idaho. J. Wildl. Manage. 44:132-144.

Kautz, L. G. 1942. Antelope survey. Colorado Wildl. Res. Quart. Prog. Rep. 8:1-26.

Kitchen, D. W. 1974. Social behavior and ecology of the pronghorn. Wildl. Monogr. 38.

Knowlton, F. F., P. E. Martin, and J. C. Haug. 1968. A telemetric monitor for determining animal activity. J. Wildl. Manage. 32:943-948.

Laundre', J. W. 1979. A behavioral study of home range utilization by coyotes on the INEL Site in southeastern Idaho. Idaho State Univ., Pocatello. Ph.D. Dissertation.

———, and B. L. Keller. 1981. Home-range use by coyotes in Idaho. Anim. Behav. 29:449-461.

Mech, L. D. 1967. Telemetry as a technique in the study of predators. J. Wildl. Manage. 31:492-496.

McBride, R., N. R. French, A. H. Dahl, and J. E. Detmer. 1978. Vegetation types and surface soils of the Idaho National Engineering. Laboratory Site. IDO-12084. National Technical Information Service, Springfield, VA.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-249.

———, and W. A. Stumpf. 1966. Comparison of methods for calculating areas of animal activity. J. Wlidl. Manage. 30:293-304.

Nace, R. L., M. Deutsch, and P. T. Vogeli. 1972. Physical environment of the National Reactor Testing Station, Idaho—a summary. U.S. Dept. Int., Geol. Surv. Prof. Paper 725-A.

———, P. T. Vogeli, J. R. Jones, and M. Deutsch. 1975. Generalized geologic framework of the National Reactor Testing Station, Idaho. U. S. Dept. Int., Geol. Surv. Prof. Paper 725-B.

Phelps, J. S. 1978. Sonoran pronghorn habitat in Arizona. Proc. Bien. Pronghorn Antelope Workshop. 8:70-77.

Prenzlow, E. J. 1965. A literature review on pronghorn behavior. Colorado Dept. Game, Fish, and Parks, and Cooperative Wildl. Res. Unit. Spec. Rep. 3.

Rongstad, O. J., and J. R. Tester. 1969. Movements and habitat use of white-tailed deer in Minnesota. J. Wildl. Manage. 33:366-379.

Sanderson, G. C. 1966. The study of animal movement—a review. J. Wildl. Manage. 30:215-235.

Slater, L. E. *ed.* 1963. Biotelemetry. Macmillan Co., New York, N.Y.
Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. J. Mammal. 35:1-15.
Woodruff, R. A. 1977. Annual dispersal, daily activity patterns, and home range of *Canis latrans* on the Idaho National Engineering Laboratory Site. Idaho State Univ., Pocatello. M.S. Thesis.
Yoakum, J. D. 1978. Pronghorn. Pages 103-121 *in* J. L. Schmidt and D. L. Gilbert, (eds.). Big Game of North America, Ecology and Management. Wildl. Manage. Inst. and Stackpole Books, Harrisburg, PA.

Received March 22, 1983
Accepted November 2, 1983

Pollene Speed

and

Gilbert B. Pauley

Washington Cooperative Fishery Research Unit[1]
College of Ocean and Fishery Sciences
University of Washington
Seattle, Washington 98195

The Susceptibility of Four Salmonid Species to the Eyefluke, Diplostomum spathaceum[2]

Abstract

Susceptibility to *Diplostomum spathaceum* differed significantly (t-test, $p = 0.05$) among rainbow trout (*Salmo gairdneri*), cutthroat trout (*Salmo clarki*), brook trout (*Salvelinus fontinalis*), and coho salmon (*Oncorhynchus kisutch*) in terms of mean survival times after exposure to orally administered cercariae. Generally, rainbow trout were the most resistant while coho salmon were the least resistant. Increased survival time of fish apparently was directly related to increased water temperature, while survival time was inversely related to dosage of cercariae administered or duration of exposure to cercariae.

Introduction

Diplostomatosis is a disease caused by metacercariae of the trematode *Diplostomum spathaceum*. It is a serious fishery management problem in many areas throughout the United States, Europe, and Africa (Palmieri *et al.* 1976b), and is a major problem in many trout waters in Idaho (Bakke 1977), Washington (Crawford 1973), Colorado (Davies *et al.* 1973), and Utah (Bakke 1977, Palmieri *et al.* 1977), where heavy aquatic vegetation allows the intermediate snail hosts to live.

The life cycle of *D. spathaceum* is fairly typical for strigeoid trematodes and has been discussed in detail by several authors (Ashton *et al.* 1969, Davies *et al.* 1973, Palmieri *et al.* 1976b, 1977). A problem in trout management arises from the fact that most members of the family Salmonidae appear to be susceptible to these eye flukes, with several members of the genera *Salmo* and *Salvelinus* reported to be infested with D. *spathaceum* (Davies *et al.* 1973; Palmieri *et al.* 1976b, 1977; Hendrickson 1978), and members of the genera *Oncorhynchus* (Bakke 1977) and *Coregonus* (Rau *et al.* 1979) infested with closely related eye flukes.

Fish are usually infected directly by motile cercariae of *D. spathaceum* penetrating the fish's integument (Davis 1936, Ratanarat-Brockelman 1974), although ingestion of metacercariae in infested snails is an alternate path of infection (Becker and Brunson 1966). Strigeoid metacercarie migrate rapidly to their target organs in the fish host (Johnson 1971, Ratanarat-Brockelman 1974) and cause severe damage both along the migration route and in the target organ, which for *D. spathaceum* is the lens of the

[1]The Unit is jointly sponsored by the University of Washington, the Washington Department of Fisheries, the Washington Department of Game, and the U.S. Fish and Wildlife Service.

[2]Contribution No. 667 from the College of Ocean and Fishery Sciences, University of Washington.

eye (Ashton *et al.* 1969, Larson 1965, Ratanarat-Brockelman 1974). Parasitization of the lens by *D. spathaceum* metacercariae can cause eye cataracts (diplostomatosis), which lead to blindness, abnormal feeding, and stunted growth (Crawford 1973, Davies *et al.* 1973, Palmieri *et al.* 1976b, 1977). Aside from mortalities that may occur after infestation (Crawford 1973, Bakke 1977, Sweeting and Powell 1977), pathological changes in individual fish cause a reduction in the overall quantity and quality of the sport catch (Davies *et al.* 1973). Therefore eye flukes have a serious potential to damage recreational trout fisheries in many areas. Since susceptibility to these parasites varies among salmonid species, it is important for successful management of fisheries to understand the differences in susceptibility. It has been found that brown trout (*Salmo trutta*) are more resistant than rainbow trout (*Salmo gairdneri*) to infestations with *D. spathaceum* (Betterton 1974, Henderson 1978). Mamer (1978) found *Diplostomum* sp. in significantly greater intensities in rainbow trout than in cutthroat trout (*Salmo clarki*). The state of Colorado stocks brown trout to take advantage of its high resistance to *D. spathaceum* (Davies *et al.* 1973).

This study was done to determine which species of salmonid fishes stocked in the state of Washington—rainbow trout (*S. gairdneri*), cutthroat trout (*S. clarki*), brook trout (*Salvelinus fontinalis*), and coho salmon (*Oncorhynchus kisutch*)—has the greatest resistance to cercarie of *D. spathaceum.*

Materials and Methods

Snails (*Lymnaea palustria* and *Physa propinqua*) were collected from aquatic vegetation in North Heron Lake in Grant County, Washington. In the laboratory, snails were kept in aquaria containing lake water at room temperature and were maintained on a diet of lettuce leaves and vegetation from their natural habitat. Live cercariae of *D. spathaceum* were readily identified under a dissecting microscope by their characteristic movements and forked tails. Approximately 3,000 cercariae could be obtained from a single infested snail by crushing the hepato-pancreas area with dissecting forceps. Special care was taken in choosing cercariae of similar maturity, as judged by size and degree of activity. Only the most active cercariae were used in experiments, while those in sporocysts were excluded. The snail, *L. palustria*, served as the laboratory source of all cercariae.

Rainbow trout, cutthroat trout, brook trout, and coho salmon averaging 15 cm in total length were used to test resistance to live cercariae. Coho salmon were obtained from the Washington Department of Fisheries hatchery at Issaquah, while cutthroat, brook, and rainbow trout were obtained from the Wahington Department of Game hatcheries at Tokul Creek, Chelan, and Arlington, respectively. Fish received an initial prophylactic Formalin treatment and were kept under laboratory conditions at least two weeks before experimental use. All fish received standard diets of salmon meal used by the hatchery at the University of Washington School of Fisheries.

Fish were artificially infested by inserting individually counted live cercariae in physiological saline into the stomach via the oral cavity with a 30-cc syringe and rubber tube (use of the tube prevented physical damage to the fish). Artificially infested fish were kept at 10° or 21°C during the experiment and signs of the disease were noted. We administered an oral dose of either 50 or 300 live cercariae to eight fish of each of the four species which were held at 15°C, and 50 cercariae to eight fish of each

species except cutthroat which were held at 21°C. Control fish received an equal volume of physiological saline administered orally.

Natural penetration of cercariae was studied in experimental fish exposed to live cercariae emerging from infested snails. An experiment using six fish of each of the four fish species was performed by exposing them to 1000 live snails of which approximately three percent were infested with emerging cercariae. Exposures were done at 21°C for either 15 min or 30 min or at 15°C for 60 min. Control fish were treated similarly in all respects except for exposure to cercariae or snails.

Results

All fish experimentally exposed to orally administered cercariae of the eyefluke died before the 270 day arbitrary end point set for these experiments. The average survival time of the four Salmonid species exposed to 50 orally administered *D. spathaceum* cercariae at 15°C differed greatly, ranging from the lowest survival average of 30 days in coho salmon to the highest of 97 days for rainbow trout (Table 1). The survival

TABLE 1. Mean survival time (days) of four species of Salmonidae after oral administration of live cercariae. Cutthroat trout were not tested at 21°C.

	Number of Cercariae and Temperature		
Species*	50 (21°C) Mean ± S.D.	50 (15°C) Mean ± S.D.	300 (15°C) Mean ± S.D.
Rainbow Trout	210 ±74.4	97 ± 8.6	40 ± 19.9
Cutthroat Trout	—	60 ± 15.9	45 ± 13.8
Brook Trout	120 ± 29.9	43 ± 9.4	56 ± 3.3
Coho Salmon	75 ±28.5	30 ± 0.7	30 ± 0.4

*Eight fish were used as controls for each species and in each experimental treatment.

times of the four species of experimental fish were significantly different (t-test, $p = 0.05$). The unexposed control fish of all four species survived until the end of the experiment (270 days), giving a significant difference (t-test, $p = 0.05$) in survival time between experimental and control fish. At increased temperature (21°C), coho salmon still survived the shortest time even though survival times for all three species tested were increased (Table 1), and these were significantly different (t-test, $p = 0.05$). Increasing the number of cercariae administered orally to 300 (Table 1), still showed coho salmon with the shortest survival (30 days), but survival time among rainbow and cutthroat trout was not significantly different (t-test, $p = 0.05$).

Using infested snails to determine the effect of exposure to emerging cercariae, we observed that rainbow trout were most resistant to cercarial penetration and that coho salmon appeared to be the least resistant (Table 2). Mean survival time declined as the exposure time was increased. At 21°C the mean survival time of all four species exposed for 30 minutes was significantly shorter (t-test, $p = 0.05$) than that of fish exposed for 15 minutes (Table 2). All control fish survived the entire experimental period.

Discussion

Determination of the most important variable is difficult, but, the survival time of fish appeared to be related to water temperature, exposure time to cercariae, and cercarial

TABLE 2. Mean survival time (days) of four species of Salmonidae exposed to snails with emerging cercariae.

Species*	Exposure Time in Minutes and Temperature 15 (21°C) Mean ± S.D.	30 (21°C) Mean ± S.D.	60 (15°C) Mean ± S.D.
Rainbow Trout	76 ± 30.0	16 ± 2.3	10 ± 0.4
Cutthroat Trout	35 ± 6.9	12 ± 2.1	9 ± 2.1
Brook Trout	62 ± 24.9	11 ± 0.4	7 ± 1.2
Coho Salmon	30 ± 7.4	12 ± 0.5	4 ± 1.2

*Six fish were used as controls for each species and in each experimental treatment.

dosage. Fish survived longer when infested at 21°C than at the lower temperature of 15°C. It is well established that fish initiate antibody formation more quickly at higher temperatures than at lower temperatures (Anderson 1974, Corbel 1975, Patterson and Fryer 1974) and there is evidence that fish form specific antibodies against metazoan parasites (Molnar and Berezi 1965, Harris 1972, Cottrell 1977). However, it is not well established how fish acquire resistance to internal metazoan parasites (Snieszko 1969, Anderson 1974). If antibodies play an active role in fish resistance to the eye fluke, then the fish may initiate a specific immune response against *D. spathaceum* more rapidly at high temperatures than at low temperatures, thereby reducing the number of cercariae that invade the fish. Higher water temperatures within the optimal temperature range should favor the fish's survival, even though cercariae are more active at higher temperatures (Becker and Brunson 1966).

In the past, chemical and physical control of the snail hosts of *D. spathaceum* have proved fruitless (Palmieri *et al.* 1976a). Until a suitable method of control is found, fishery biologists should consider the high resistance of certain species of Salmonidae to *D. spathaceum* as a management tool. The significant observation for management purposes is that coho salmon were always the first fish to die and that rainbow trout were generally the most resistant to *D. spathaceum*. From our results, coho salmon would probably give fewer returns to the angler as compared to rainbow trout. Cutthroat trout or brook trout would be a secondary choice to stock if rainbow trout were not available. If feasible from an economic and sport point of view, brown trout would seem to be an even better choice than rainbow trout (Davies *et al.* 1973, Betterton 1974). Crawford (1973) has indicated that stocking legal size trout in known infested waters would also help provide a good sport fishery.

Acknowledgments

We thank the following people for reviewing and evaluating the manuscript: Dr. C. D. Becker, Battelle Northwest, Richland, Washington; Dr. G. A. Wedemeyer, National Fisheries Research Laboratory, Seattle, Washington; and Dr. R. R. Whitney, Washington Cooperative Fishery Research Unit, Seattle, Washington.

Literature Cited

Anderson, D. P. 1974. Fish Immunology. T.F.H. Publications, Inc. Neptune City, New Jersey.
Ashton, N., N. Brown, and D. Easty. 1969. Trematode cataract in freshwater fish. J. Small Anim. Pract. 10: 471-478.
Bakke, B. M. 1977. Flukes kill fish. Salmon, Trout, Steelhead Magazine, April-May.
Becker, C. D., and W. Brunson. 1966. Transmission of *Diplostomum flexicaudum* to trout by ingestion of precocious metacercariae in molluscs. J. Parasitol. 52: 829-830.

Betterton, C. 1974. Studies on the host specificity of the eyefluke, *Diplostomum spathaceum*, in brown and rainbow trout. Parasitology 69: 11-39.
Corbel, M. J. 1975. The immune response in fish: a review. J. Fish. Biol. 7: 539-563.
Cottrell, B. 1977. The immune response of plaice (*Pleuronectes platessa* L.) to the metacercariae of *Crytocotyle lingua* and *Rhipidocotyle johnstonei*. Parasitology 74: 93-107.
Crawford, B. A. 1973. *Diplostomum spathaceum* (Rudolphi), the Cause of Chronic Fish Mortalities at Waitts Lake, Washington. University of Washington, Seattle. M.S. Thesis.
Davies, R. B., W. T. Burkhard, and C. P. Hibler. 1973. Diplostomiasis in North Park, Colorado. J. Wildlife Dis. 9: 362-367.
Davies, D. L. 1936. Pathological studies on the penetration of the cercariae of the strigeoid trematode, *Diplostomum flexicaudum*. J. Parasitol. 23: 329-337.
Harris, J. E. 1972. The immune response of a cyprinid fish to infections of the acanthocephalan *Pomphorhynchus laevis*. Internatl. J. Parasitol. 2: 459-469.
Hendrickson, G. L. 1978. Observations on strigeoid trematodes from the eyes of southeastern Wyoming fish. I. *Diplostomum spathaceum* (Rudolphi, 1819). Proc. Helminthol. Soc. Wash. 45: 60-64.
Johnson, K. A. 1971. The migration of *Cotylurus erraticus* cercariae (Trematoda: Strigeidae) in rainbow trout (*Salmo gairdneri*) and their effects on the host. J. Parisitol. 57: 244-251.
Larson, O. R. 1965. *Diplostomum* (Trematoda: Strigeoidae) associated with herniations of bullhead lenses. J. Parasitol. 51: 224-229.
Mamer, B. E. 1978. The parasites of trout in northwest Washington. J. Parasitol. 64: 314.
Molnar, K., and I. Berezi. 1965. Nachweis von parasitenspecifischen Antikörpen im Fishchblut mittels der Agar-Gel-Präzitationsprobe. Zeit. Immunitäts Allergieforsch. 129: 263-267.
Palmieri, J. R., A. Coli, and R. A. Heckman. 1976a. Experimental biological control of the eye fluke, *Diplostomum spathaceum*, by a protozoan hyperparasite, *Nosema strigeodeae* (Protozoa: Microsporida). J. Parasitol. 62: 325-326.
———, R. A. Heckman, and R. S. Evans. 1976b. Life cycle and incidence of *Diplostomum spathaceum* Rudolphi (1918) (Trematoda: Diplostomatidae) in Utah. Great Basin Natural. 36: 86-96.
———, ———, and ———. 1977. Life history and habitat analysis of the eye fluke *Diplostomum spathaceum* (Trematoda: Diplostomatidae) in Utah. J. Parasitol. 63: 427-429.
Paterson, W. D., and J. L. Fryer. 1974. Effect of temperature and antigen dose on the antibody response of juvenile coho salmon (*Oncorhynchus kisutch*) to *Aeromonas salmonicida* endotoxin. J. Fish. Res. Bd. Can. 31: 1743-1749.
Ratanarat-Brockelman, C. 1974. Migration of *Diplostomum spathaceum* (Trematoda) in fish intermediate hists. Zeit. Parasitenk 43: 1743-1749.
Rau, M. E., D. M. Gordon, and M. A. Curtis. 1979. Bilateral asymmetry of *Diplostomum* infections in the eyes of lake whitefish *Coregonus clupeaformis* (Mitchill) and a computer simulation of the observed metacercarial distribution. J. Fish Dis. 2: 291-297.
Snieszko, S. F. 1969. Cold-blooded vertebrate immunity to Metazoa. Pages 267-275 *In* Jackson, Herman, and Singer (Eds.) Immunity to Parasatic Animals. Appleton-Century-Crofts, New York.
Sweeting, R. A., and A. Powell. 1977. Mortalities of fish associated with eye flukes. Parasitology 75: xxxviii.

Received March 25, 1983
Accepted July 2, 1983

Association News

Research Grants/Research Funds

Applications for research grants for 1985 should be mailed to the secretary of the Northwest Scientific Association no later than February 1, 1985. Successful applicants will be notified by April 1. For more information or application forms write to: Robert L. Carr, Secretary, NWSA, Department of Biology, Eastern Washington University, Cheney, Washington 99004.

All members are encouraged to make voluntary contributions to the NWSA Research Fund at any time. These funds assist the NWSA in providing annual research grants. Contact Steve Brunsfeld, Treasurer.

Honorary Awards

The Board of Trustees is soliciting nominations for the NWSA "Outstanding Scientist" and "Honorary Life Member" awards. We encourage you to help our Awards and Honors Committee in their search for outstanding candidates. Contact the NWSA Secretary at the above-listed address.

1985 Annual Meeting

The 58th Annual Meeting of the Northwest Scientific Association will beheld at the Gage Residence and Conference Center of the University of British Columbia, Vancouver, B.C. Canada, May 22-24, 1985. The call for papers and detailed general information concerning the meeting will be distributed soon.

Meetings

Joint meetings of the Herpetologist's League and the Society for the Study of Amphibians and Reptiles (HL/SSAR), University of South Florida, Tampa, Florida, August 3-9, 1985. For further information write: Henry R. Mushinsky, Department of Biology, University of South Florida, Tampa, Florida 33620.

Correction

In paragraph 3 of the Annual Meeting News reported on page 162 of Volume 58, Number 2 of *Northwest Science*, Dr. Te May Ching was incorrectly cited as an honorary life member of the organization. Instead, Dr. Ching was named "Scientist of the Year."

Reviewers of Articles for Volume 58

Heartfelt thanks from the editors is hereby extended to the reviewers who served *Northwest Science* so well during 1984.

C. Melvin Aikens, University of Oregon.
Dorald Allred, Brigham Young University
David C. Barnes, Washington State University
Paul Baxter, BC/AD Consultants, Eugene, Oregon
Paul Catts, Washington State University
Anita Cholewa, Washington State University
Tom Connolly BC/AD Consultants, Eugene, Oregon
Roger del Moral, University of Washington
Charles H. Driver, University of Washington
Richard Dunn, Natural Marine Fisheries Service, Seattle, Washington
D. Easterbrook, Western Washington University
Carleton B. Edminster USDA-Forest Service, Fort Collins, Colorado
Robert B. Ferguson, USDA-Forest Service, Provo, Utah
Richard Fitzner, Battelle-Pacific Northwest Laboratories
Jarran Flinders, Brigham Young University
Amy J. Gilmartin, Washington State University
Carl Gustafson, Washington State University
Paul Heilman, Washington State University
Richard Hutto, University of Montana
Kenneth V. Kardong, Washington State University
James R. King, Washington State University
Eugene Kozloff, University of Washington
Dean Medin, USDA-Forest Service, Boise, Idaho
Evelyn Merrill, University of Washington
R. A. Monserud, USDA-Forest Service, Moscow, Idaho
Robert B. Murray, USDA-Agricultural Research Service, Dubois, Idaho
Louis Nelson, Idaho Fish and Game Department, Boise, Idaho
Dale C. Perry, University of Idaho
Michael Samuels, University of Idaho
D. R. Satterlund, Washington State University
Mark Stallmaster, ERO Research Corporation, Golden, Colorado
Ken Swedborg, Eastern Washington University
J. Mary Taylor, Portland, Oregon
Ronald Taylor, Western Washington University
Gary Thorgaard, Washington State University
Arthur R. Tiedmann, Pacific Forest and Range Experiment Station, LaGrande, Rregon
B. J. Verts, Oregon State University
Daniel J. Vogt, University of Washington
Peter Zagler, Idaho Fish and Game Department, Coeur d'Alene, Idaho
Don Zobel, Oregon State University

(Apologies, as well as thanks, to any reviewers that we inadvertently omitted).

Northwest Science

Volume 58, 1984

John W. Weber and H. Clare Wiser, Editors

Published by Northwest Scientific Association in collaboration with the Washington State University Press.

Contents

Number 1 (February)

A Late Quaternary Chronology of Mass Wasting for a Small Valley in the Lemhi Mountains of Idaho 1
David R. Butler

Lead Concentrations in Ruffed Grouse Collected from Southwestern Virginia 14
Ronald J. Kendall, Gary W. Norman, and Patrick F. Scanlon

Analysis of Surface Pollen from Alberta, Canada, by Polar Ordination 18
Richard G. Holloway

An Approach to Classifying Seral Vegetation within Habitat Types 29
Robert Steele

Distribution, Abundance, and Nesting Characteristics of Snowy Plovers on the Oregon Coast 40
Ruth Wilson-Jacobs and E. Charles Meslow

Histology of **Cowania stansburiana** Actinorhizae 49
David L. Nelson and Pattie L. Schuttler

Early Plant Succession on Pinyon-Juniper Controlled Burns 57
Richard L. Everett and Kenneth Ward

The Recent History and Present Distribution of the Red Fox in Washington 69
Keith B. Aubry

Vegetation Types Used by Mule Deer Fawns, Mid-Columbia River, Washington 80
Paul C. Fielder and Charles E. McKay, Jr.

Meetings 79

1983 Manuscript Reviewers 79

Number 2 (May)

Chemical Content of Snow and Effect of Melting on Cascade Mountain Lakes 85
Eugene B. Welch, William H. Chamberlain, and Dimitris E. Spyridakis

Indian Basin Advance in Western and North-Central Wyoming 94
W. C. Mahaney

Lead Shot Ingestion in Waterfowl in Washington State, 1978-1979 103
Crystal J. Driver and Ronald J. Kendall

The Zonation of Mosses and Lichens Along the Salmon River in Idaho 108
Roger Rosentreter

Biology of Smallmouth Bass **(Micropterus dolomieui)** in Lake Sammamish, Washington 118
David E. Pflug and Gilbert B. Pauley

A Comparison of Structural Properties and Compositional Trends in Conifer Forests of Yosemite and Glacier National Parks, USA 131
Albert J. Parker

Parasitic Mites of Voles of the genera **Microtus** and **Clethrionomys** from Oregon 142
John O. Whitaker Jr., and Chris Maser

Comments on an Apparent Sharp-Tailed Grouse Movement in Eastern Montana 151
Irven O. Buss

Lice **(Mallophaga** and **Anoplura)** from Mammals of Oregon 153
K. C. Emerson, Chris Maser, and John O. Whitaker, Jr.

Association News 162

Northwest Science Index; Meetings; Announcement

Number 3 (August)

Aquatic Oligochaeta **(Naididae)** of Washington 165
Michael E. Smith

Relative Abundance of Small Mammals in Four Successional Stages of Spruce-Fir Forest in Idaho 171
Jerry H. Scrivner and H. Duane Smith

Free-swimming Invertebrate Communities of Vernal Pools in Eastern Washington 177
Robert L. Kulp and Fred W. Rabe

Ultimate Loads for Shallow Funicular Concrete Shells 187
John W. Weber, Kwong-Chi Wu, and Abholhassan Vafai

Bryozoan Behavior in Relation to Autocleaning in **Holoporella brunnea** (Hincks) 195
Matthew H. Dick

Vaccinium Membranaceum Berry Production Seven Years After Treatment to Reduce Overstory Tree Canopies 208
Don Minore

New, Rare, and Unusual Algae from Montana 213
Daniel Wujek and James L. Wee

Temperature Characteristics, Annual Heat Storage, and River Diversion Influence on a Monomictic Lake 222
Thomas J. Loranger and David Brakke

Nesting Ecology of Mourning Doves in Fruit Orchards in North-Central Washington 230
Richard L. Knight, Dwight G. Smith, David M. Gaudet, Albert W. Erickson

Selected Avian Systematic Problems in the Northwest: The 1983 A. O. U. Check-list 237
John T. Ratti

Number 4 (November)

A Comparison of Periphyton Growth on Artificial and Natural Substrates in the Upper Spokane River 243
Thomas S. Nielsen, William H. Funk, Harry L. Gibbons, and Robert M. Duffner

The Variation in Antagonistic **Streptomyces** Populations in Soils from Different Vegetation Types in Western Oregon 249
Anita Stiebrs Hutchins and Sharon L. Rose

A Method for Estimating Precipitation Amounts at Remote Field Sites 256
Robert R. Kindschy

Using Isozyme Analysis to Aid in Selecting Genetically Superior Ponderosa Pine for Coal-Mine Spoil Reclamation 262
Jack H. Woods, George M. Blake, and Fred W. Allendorf

Glaciation in the Lower Lewis River Basin, Southwestern Cascade Range, Washington 269
Maurice J. Mundorff

Demise of Spiny Hopsage Shrubs Following Summer Wildfire: An Authentic Record 282
W. H. Rickard and M. C. McShane

The Status of Wolverines in Colorado 286
David M. Nead, James C. Halfpenny, and Steve Bissell

Age-specific Productivity and Nest Site Characteristics of Cooper's Hawks **(Accipiter cooperii)** 290
Kevin R. Moore and Charles J. Henny

Daily Summer Movements, Activity Patterns, and Home Range of Pronghorn 300
Timothy D. Reynolds

The Susceptibility of Four Salmonid Species to the Eyefluke, **Diplostomum spathaceum** 312
Pollene Speed and Gilbert B. Pauley

Association News; Miscellaneous Announcements 317

Honorary Life Members

William H. Baker
Ewart M. Baldwin
Julian B. Barksdale
Irven O. Buss
L. C. Cady
Charles D. Campbell
Julian L. Culbertson
Rexford Daubenmire
Glenn Deitschman
R. A. Diettert
Bruce V. Ettling
William T. Ferrell
C. Clement French
Stanley P. Gessel
N. S. Golding
Phil Haddock
H. P. Hansen
Adolph Hecht
Kenneth Holmes
G. Brooks King
Rufus W. Kiser
Lewis and Clark High School Library (in memory of Thomas Large and J. G. McCracken)
Ernest Lund
Willis B. Merriam
Joseph W. Mills
Milton M. Mosher
Richard J. Naskali
Frank D. Nicol
Frances J. Schadegg
C. Gardner Shaw
Leona M. Sundquist
Robert F. Tarrant
Richard B. Walker
D. J. Wort

1984 Sustaining Institutional Members

Battelle Northwest, Richland, Washington
EG&G Idaho, Inc., Idaho Falls, Idaho
MacMillan Bloedel, Ltd., Nanaimo, British Columbia, Canada
Potlatch Corporation, Lewiston, Idaho
The Washington Water Power Company, Spokane, Washington
Weyerhaeuser Company, Centralia, Washington

1984 Institutional Members

Boise State University, Boise, Idaho
British Columbia Institute of Technology, Burnaby, British Columbia, Canada
Central Oregon Community College, Bend, Oregon
Central Washington University, Ellensburg, Washington
Centralia College, Centralia, Washington
College of Idaho, Caldwell, Idaho
Eastern Montana College, Billings, Montana
Eastern Oregon State College, LaGrande, Oregon
Eastern Washington University, Cheney, Washington
Edmonds Community College, Lynwood, Washington
The Evergreen State College, Olympia, Washington
George Fox College, Newberg, Oregon
Grays Harbor College, Aberdeen, Washington
Green River Community College, Auburn, Washington
Highline Community College, Midway, Washington
Idaho State University, Pocatello, Idaho
Lewis-Clark State College, Lewiston, Idaho
Lewis and Clark College, Portland, Oregon
Linfield College, McMinnville, Oregon
Montana College of Mineral Science and Technology, Butte, Montana
Mt. Hood Community College, Gresham, Oregon
North Idaho College, Coeur d'Alene, Idaho
Oregon Institute of Technology, Klamath Falls, Oregon
Oregon State University, Corvallis, Oregon
Pacific Lutheran University, Tacoma, Washington
Pacific University, Forest Grove, Oregon
Peninsula College, Port Angeles, Washington
Portland State University, Portland, Oregon
Saint Martin's College, Lacey, Washington
Seattle Central Community College, Seattle, Washington
Seattle Pacific University, Seattle, Washington
Shoreline Community College, Seattle, Washington
Simon Fraser University, Burnaby, British Columbia, Canada
Skagit Valley College, Mount Vernon, Washington
Southern Oregon State College, Ashland, Oregon
Southwestern Oregon Community College, Coos Bay, Oregon
Spokane Falls Community College, Spokane, Washington
University of Alaska, Fairbanks, Alaska
University of Idaho, Moscow, Idaho
University of Montana, Missoula, Montana
University of Puget Sound, Tacoma, Washington
University of Victoria, Victoria, British Columbia, Canada
University of Washington, Seattle, Washington
Walla Walla College, College Place, Washington
Washington State University, Pullman, Washington
Western Oregon State College, Monmouth, Oregon
Western Washington University, Bellingham, Washington
Whitman College, Walla Walla, Washington
Whitworth College, Spokane, Washington
Yakima Valley College, Yakima, Washington

1984 Sustaining Individual Members

R. Michael Anthony, Bend, Oregon
Stephen F. Arno, Florence, Montana
Donald J. Brown, Richland, Washington
Randall E. Brown, Pasco, Washington
Nelsa M. Buckingham, Port Angeles, Washington
Robert L. Carr, Cheney, Washington
Tim W. Clark, Jackson, Wyoming
Richard G. Cline, Missoula, Montana
Susan G. Conrad, Corvalis, Oregon
George W. Douglas, Victoria, British Columbia, Canada
Arlene T. Doyle, Arcata, California
George R. Fahnestock, Seattle, Washington
William R. Funk, Pullman, Washington
Tom Gnojek, Soda Springs, Idaho
Gerald H. Haddock, Wheaton, Illinois
Frederick C. Hall, Portland, Oregon
Mary M. Hektner, Arcata, California
Charles R. Hatch, Moscow, Idaho
Francis R. Herman, Fairbanks, Alaska
Robert J. Jonas, Moscow, Idaho
Barry L. Keller, Pocatello, Idaho
John H. Larsen, Pullman, Washington
Denis P. Lavender, Corvallis, Oregon
Cal E. Meier, College Station, Texas
John E. Mitchell, Fort Collins, Colorado
Emmett B. Moore, Jr., Richland, Washington
Howard R. Panik, Carson City, Nevada
William H. Rickard, Richland, Washington
Edward S. Schreiner, Port Angeles, Washington
Dale Stradling, Cheney, Washington
Ronald J. Taylor, Bellingham, Washington
Ralph L. Thompson, Berea, Kentucky
David D. Tillson, Salt Lake City, Utah
James M. Thorpe, Corvallis, Oregon
Daniel W. Uresk, Rapid City, South Dakota
Shepard M. Zedeker, Christiansburg, Virginia

Non-Profit Org.
BULK RATE
U.S. POSTAGE
PAID
PULLMAN, WA
Permit No. 1

US ISSN 0029 344X

Northwest Science

Quarterly Publication of the Northwest Scientific Association

Editor H. Clare Wiser Washington State University

Associate Editors

Botany	Robert L. Carr	Eastern Washington University
Chemistry and Physics	Frank L, Curzon	University of British Columbia
Engineering and Mathematics	Gary L. Sheldon	Washington State University
Forestry	Warren P. Clary	U.S. Forest Service
Geology	Franklin F. Foit, Jr.	Washington State University
Social Sciences	Phillip D. Young	University of Oregon
Soils	Robert L. Edmonds	University of Washington
Zoology	Donald R. Johnson	University of Idaho

Papers published in *Northwest Science* are indexed in *Current Contents, Science Citation Index, Biological Abstracts, The Zoological Record, Recent Literature Supplement to The Auk, Abstracts in Anthropology, Bibliography and Index of Geology, Chemical Abstracts, Bibliography of Agriculture, Forestry Abstracts,* and *University Microfilms.*

Northwest Science is offered in exchange to other colleges, universities, learned societies, and libraries. Publications sent in exchange should be addressed to Washington State University Library, Technical Services Division, Pullman, Washington 99164-5610, U.S.A.